



An illustrated checklist of the genus *Elymnias* Hübner, 1818 (Nymphalidae, Satyrinae)

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Abstract

We review the genus *Elymnias* Hübner, 1818, a morphologically diverse satyrine butterfly clade involved in multifarious Batesian mimicry relationships throughout Asia and Africa. A variety of different model species are mimicked, and many *Elymnias* species are sexually dimorphic mimics, with males and females resembling different model species. We revise species and subspecies delimitations in light of an integrative taxonomic investigation using external morphology, male and female genital morphology, and a multilocus molecular phylogeny. There is little interspecific genitalic variation among species in this group, and previous taxonomists therefore relied almost entirely on wing patterns. Our molecular phylogenetic analysis reveals several examples of polymorphism or wing pattern divergence within a single species currently classified as two or more different species. We also found examples of wing pattern convergence among disparate lineages that mimic the same widespread model species. Frequently, two or more phenotypically similar species were classified as a single species. This comprehensive checklist reviews all names associated with *Elymnias* to align its taxonomy with the evolutionary history of the group. All available information on nomenclature, type localities, repositories of type specimens, and geographical distributions is summarized, and images of adult specimens and genitalia are provided along with distribution maps of all species and selected subspecies. We identify 2 species incertae sedis, establish 15 monophyletic species groups (including 1 species unplaced in any species group), and make 49 taxonomic changes, including 35 new synonyms, 7 new combinations (2 of which have new status), 1 resurrected combination, 1 resurrected subspecies, and 7 status changes.

Keywords

Batesian mimicry, convergent evolution, Elymniini, polymorphism, sexual dimorphism, Southeast Asia

Introduction

Elymnias Hübner, 1818 (Nymphalidae: Satyrinae) is a species-rich and widespread butterfly genus distributed throughout the Old World tropics (Aoki et al. 1982). It derives its name from Elymnias jynx Hübner, 1818 (now Elymnias hypermnestra hypermnestra (Linnaeus, 1763)) (Fruhstorfer 1907). The genus' widespread range and remarkable wing pattern diversity, together with the economic importance of several species, has attracted the attention of taxonomists and agricultural entomologists for centuries (Merrett 1993; Wallace 1869). However, the entire group has not been examined systematically in over 100 years (Fruhstorfer 1907; 1911), and no studies to date have used genetic data to substantiate taxonomic hypotheses. Most species are found in the Indo-Australian Archipelago, a geographically complex and geologically dynamic area with over 20,000 islands that are likely to have contributed to diversification in this taxon (Lohman et al. 2011).

We recognize a single Afrotropical species with two subspecies and 52 Australasian species with 181 subspecies distributed from Nepal to Sri Lanka in the west, throughout tropical and subtropical Asia, and extending east to Taiwan and south to Australia's Cape York and the Bismark Archipelago of Papua New Guinea. A few species are widespread across several countries or landmasses, but many are restricted to single islands. Several new species have been discovered recently (Monastyrskii 2004; Okubo 2010; Saito and Koshi 2012), highlighting the rarity of many species and their predilection for relatively inaccessible locales, such as high mountains and remote islands.

Species in the genus differ markedly in wing color, pattern, shape, and size, making *Elymnias* one of the most morphologically heterogeneous butterfly genera (Feltwell 1993). This morphological diversity is apparently because most species are Batesian mimics of strikingly different, unpalatable model butterfly species (Corbet 1933; 1943). Many *Elymnias* species are monomorphic; conspecific males and females mimic the same model species (*e.g.*, *E. paradoxa* and *E. vasudeva*). However, some species are sexually dimorphic mimics (Moore 1894; Punnett 1915; Vane-Wright 1976), with males and females mimicking different models and differing markedly in wing color and pattern (*e.g.*, *E. kuenstleri* and *E. harterti*; Corbet et al. 1992; Parsons 2000). A few sexually dimorphic *Elymnias* species mimic a single sexually dimorphic model species, such as *E. casiphone* and *E. saueri*, which both mimic *Euploea mulciber*. A few species exhibit variability in sexual dimorphism: males and females in some populations mimic the same model species and are monomorphic, while the same species is strongly dimorphic in other locales (*e.g.*, *E. hypermnestra* and *E. agondas*).

Larvae of all species with known life histories feed exclusively on palms (Arecaceae) (Bascombe et al. 1999; Ek-Amnuay 2012; Parsons 2000; Robinson et al. 2017), and several species are also agricultural pests on economically important oil palm, *Elaeis guineensis*

(Koh and Gan 2007; Merrett 1993). Adults are known to feed on exudates from rotting fruit (Treadaway and Schroeder 2012). Palm-feeding butterflies are not known to sequester noxious secondary compounds from their larval hosts, and naïve avian predators readily consumed adult *E. hypermnestra* in laboratory trials (S.-H. Yen, unpublished results), supporting the hypothesis that *Elymnias* are Batesian and not Müllerian mimics.

After the description of Linnaeus's Papilio hypermenstra (now Elymnias hypermnestra hypermnestra) in 1763, the accumulation of new species/subspecies publications was slow and confined to few localities, for instance, E. nesaea (Linnaeus, 1764) from Java, E. panthera (Fabricius, 1787) from Borneo, and E. vitellia (Stoll, [1781]) from Ambon. Most species and subspecies were described during between the middle of the 19th century and early 20th century in the following works: Hewitson (1858; 1861; 1867; 1874; South East Asian Islands), Felder and Felder (1860; 1863; 1867; Philippines), Butler (1867; 1871; 1874; 1882; 1883; Asia), Distant (1882a; b; 1883; 1886; Malaysia), Semper (1887; 1892; Philippines), Grose-Smith (1889; 1892; 1894a; b; 1897; South East Asian Islands), Staudinger (1889; 1894a; b; Palawan and New Guinea), de Nicéville (1890; 1893; 1895; 1898; 1900; 1902; Indo-Malaya), Moore (1857; 1875; 1878a; b; 1880; 1886; 1894; Indian subcontinent and Indochina), Fruhstorfer (1894a; b; c; 1895a; b; 1896a; b; c; 1898a; b; c; 1899; 1900; 1902a; b; c; 1904a; b; c; d; Southeast Asia; 1911), Rothschild (1915a; b; c; d; islands surrounding New Guinea), Hemming (1967; global), and Talbot (1929; 1932; Malaysia). Several new taxa have been discovered during the last 40 years, including species described by Jumalon (1975; Philippines), Tsukada and Nishiyama (1979; Southeast Asia), Tateishi (2001; Southeast Asia), Uémura and Kitamura (2001; Philippines), Monastyrskii (2004; the Indochina), Suzuki (2006; the Andaman Islands), Okubo (2010; the Lesser Sunda Islands), and Saito and Koshi (2012; Indochina).

The first checklist of *Elymnias* was compiled by Wallace (1869), followed by Butler (1871); Gaede (1931) enumerated the *Elymnias* species recognized at that time. The most recent comprehensive generic revision was completed by Fruhstorfer (1907; 1911), who recognized over 200 species-level taxa. This most recent study established the genus' higher classification, infrageneric grouping, geographical distributions, diagnostic characters, and synonyms. He recognized *Elymniopsis* Westwood, [1851] (now a junior synonym of *Elymnias*) as a valid genus and separated *Elymnias* into two subgenera: Elymnias and Mimadelias Moore, 1894. However, Fruhstorfer's taxonomic treatment relied entirely on comparisons of wing shape and color pattern; he did not examine genitalia. After this work, a few additional publications provide regional checklists with images of adults, including: Aoki and Uémura (1982), D'Abrera (1985), Pinratana (1988), Corbet et al. (1992), Osada et al. (1999), Chou (2000), Monastyrskii (2005), Ek-Amnuay (2012), Treadaway and Schroeder (2012), and Inayoshi (2017). These works, together with G. Lamas' catalog of butterfly names established the taxonomic groundwork for the genus. Prior to the present study, ca. 47 species and 190 subspecies were recognized (G. Lamas, pers. comm.).

This checklist enumerates and verifies all current combinations and synonyms, and provides original literature citations, type localities, repositories of type specimens,

photographs of specimens and genitalia, and maps of each subspecies' geographical range and type locality. Integrative taxonomic practice employing multi-locus molecular phylogenetics in concert with data from wing and genitalic characters has informed taxonomic decisions to retain or revise contentious classification and nomenclature. This checklist is meant to clarify taxonomic problems in the genus and aid biologists interested in studying butterfly biodiversity, but will also serve as a framework for future studies on the phylogeny, biogeography, wing pattern evolution, and speciation of this fascinating radiation of Batesian mimetic butterfly species.

Material and methods

Examination of original literature and type specimens

The taxonomic changes we propose are based on examinations of hundreds of specimens in dozens of museums, quantification of wing and genitalic characters including over 100 dissections of males and females (Wei et al. in prep.), and a multi-locus molecular phylogenetic analysis based on six genetic markers from over 200 specimens including nearly every species that we recognize (Lohman et al. in prep.).

Verification of type specimens was based on information provided in the original literature as well as critical review of the collection of specific authors, especially Fruhstorfer. All taxonomic treatments proposed in the present study, including the availability of infrasubspecific taxa, follow regulations and suggestions of the latest version of ICZN (1999).

All publications with original descriptions of new taxa or describing new taxonomic acts were consulted to verify the status and collection localities of type material. Geographical information was obtained directly from specimen labels and from literature to provide accurate locality data and minimize misinterpretation of geographical localities caused by misidentified or mislabeled specimens.

All images of specimens photographed in various museum collections are used here with permission from each museum. Except for the photographs provided by KUTH (Department of Entomology, Kasetsart University), David J. Lohman, and the Museum of Comparative Zoology, Harvard University, all the other photographs were taken by Chia-Hsuan Wei and Shen-Horn Yen.

The following abbreviations are used to specify the repository of type material. Specimens, including type specimens, were borrowed and/or photographed from many of these institutions and private collections.

Abbreviations of specimen repositories

DNPFIC Forest Insect Collection, Department of National Parks, Wildlife and Plant Conservation, Thailand

ECMP Entomology Collection, Bureau of Science, Manila, Philippines

FMNH Field Museum of Natural History, Chicago, USA

HPC Hiroto Hanafusa Private Collection, JapanHSPC Hiroyuki Soeda Personal Collection, Japan

IM Indian Museum, Calcutta, India

IPC Yutaka Inayoshi Private Collection, Chiang Mai, ThailandJPC Julian Jumalon Private Collection, Cebu City, Philippines

KMSPC Kazu-Michi Suzuki Private Collection, Japan

KUTH Department of Entomology, Kasetsart University, Thailand

LSL Linnaean Society of London, London, UK

MCZ Museum of Comparative Zoology, Harvard University, USA

MEPR Museo Entomologico Pietro Rossi, Duino, Italy NODAI Tokyo University of Agriculture, Tokyo, Japan

MUS Malaysia Universiti Sarawak, Kota Samarahan, Malaysia

NBC National Biodiversity Center, Leiden, Netherlands

NHM The National History Museum, London, UK

NHMT The National History Museum at Tring, Tring, UK Vienna Museum of Natural History, Vienna, Austria

NMNH National Museum of Natural History, USA

NRM Naturhistoriska Riksmuseet, Stockholm, Sweden

NSYSU National Sun Yat-Sen University, Kaohsiung, Taiwan

NWSUAF Northwest A & F University, Shaanxi, ChinaOMPC Kikumaro Okano Private Collection, JapanOPC Kiyoshi Okubo Private Collection, Japan

PNM National Museum of the Philippines, Manila, PhilippinesSMFD Naturmuseum Senckenberg, Frankfurt am Main, Germany

SMK Sarawak Museum Kuching, Sarawak, Malaysia

SMTD Staatliches Museum für Tierkunde, Dresden, Germany

SPC Kotaro Saito Private Collection, Japan

TME Toyosato Museum of Entomology, Tsukuba, Japan

TPC Tsukada Private Collection, Japan

UPC Yoshinobu Uémura Private Collection, JapanZMHB Museum für Naturkunde, Berlin, Germany

ZMUC Zoological Museum University of Copenhagen, Copenhagen, Denmark

Species concept and integrative taxonomic approach

We ascribe to the Biological Species Concept, which defines species as reproductively isolated groups of populations (Mayr 1940). We have attempted to recognize reproductive isolation between species by identifying coordinated morphological and/or genetic differences among species in several traits. We also expect that species should not be polyphyletic and that species should generally be monophyletic after sufficient

time since divergence from their sister taxon. We regard subspecies as phenotypically distinctive geographic variants and do not expect them to be monophyletic or reproductively isolated from other subspecies (Braby et al. 2012). However, a subspecies should be differentiable from other conspecific subspecies using morphology, genetic data, or other characteristics.

Given the within-species morphological variability known from this and other mimetic butterfly taxa (Punnett 1915), we adopted the following procedures for evaluating the validity of prior taxonomic hypotheses: (1) We reconstructed phylogenies using both morphological (Wei et al. in prep.) and molecular data (Lohman et al. in prep.), and used these as guides for interpreting relationships among species and taxonomic boundaries within species complexes; (2) In these analyses, we endeavored to include specimens from the type localities (or the surrounding area—at least the same island group) of the nominotypical subspecies to substantiate taxonomic boundaries of geographically widespread species with multiple subspecies (e.g., agondas, casiphone, hypermnestra, nesaea, and panthera); (3) We considered the geological history of a species' range (Hall 2001; Hall and Smyth 2008; Sathiamurthy and Voris 2006), particularly for taxa that are rare in museum collections and not readily available for morphological or molecular study. For example, present-day Sulawesi comprises multiple terranes, some of which originated in different biogeographical subregions, that collided in the Miocene (Lohman et al. 2011; Stelbrink et al. 2012). If two or more subspecies of the same species are described from a large and geologically complex island such as Sulawesi or New Guinea and we had limited material for phylogenetic study, then we generally retained the landmass's different subspecies for lack of evidence to synonymize them; (4) When genetic and/or ecological data suggested that different names had been applied to different mimetic forms, sexes, or seasonal forms, we synonymized these taxa.

For convenience, we have divided the genus into 15 monophyletic species groups (Lohman et al. in prep.) named after each clade's oldest named species. Because of the uniformity of genitalia and extreme intraspecific variability in wing patterns, there are few if any morphological synapomorphies that can be used to discriminate these species groups. They have been circumscribed based on relatedness as inferred by a multilocus molecular phylogeny.

Distribution maps and type localities

A variety of sources were used to infer the distribution maps that we provide, including museum data, taxonomic and other publications (Aoki et al. 1982; Braby 2000; Ek-Amnuay 2012; Hanafusa 2001; Inayoshi 2017; Monastyrskii 2004; 2005; Okubo 2010; Parsons 2000; Saito and Koshi 2012; Suzuki 2006; Tateishi 2001; Treadaway and Schroeder 2012; Uémura and Kitamura 2001; Vane-Wright and de Jong 2003). The majority of *Elymnias* taxa were described when most of South and Southeast Asia were colonized by European countries, and many of the type locality names given in the species descriptions have changed since colonial times. Therefore, in addition to

the original type locality names given in the species description, we have attempted to provide the modern locality names in parentheses. In the text below, we do not attempt to use present knowledge of the taxon's distribution to infer the precise location where the type was collected. However, when designating type localities on the distribution maps, we have attempted to use knowledge of the taxon's current distribution and other information to indicate the type locality as precisely as possible. Nonetheless, many type localities are imprecise and cannot be localized because many labels simply list the island where the specimen was found (e.g., New Guinea) rather than a precise locality.

Format of the checklist

This annotated checklist is formatted in the following way:

valid species name author, year

Specimens: Figs X, Y, Z; Male Genitalia: Figs X, Y, Z; Distribution: Fig: X

ssp. recognized valid subspecies name, author, year

Original combination of subspecies, Author, Year. **TL:** Type locality provided in original description (Current name of type locality in a standardized format-Country: Province, locality). **TS:** Depository of type specimen. Original citation.

Junior synonym original combination, Author, Year. **TL:** Type locality provided in original description (Current name of type locality); **TS**: Depository of type specimen. Original citation.

Checklist of Elymnias

ELYMNIAS Hübner, 1818 (Type species: Elymnias jynx Hübner, 1818, = Papilio

hypermnestra Linnaeus, 1763) Zuträge Samml. exot. Schmett. 1:12.

Didonis Hübner, [1819] (Type species: Papilio vitellia Stoll, 1781)1

Verz. bek. Schmett. 2: 17.

Dyctis Boisduval, 1832 (Type species: Dyctis agondas Boisduval, 1832)

Voy. Astrolabe. 1: 138.

Agrusia Moore, 1894 (Type species: Melanitis esaca Westwood, 1851)

Lepidoptera Indica 2 (18): 169.

Bruasa Moore, 1894 (Type species: Melanitis penanga Westwood, 1851)

Lepidoptera Indica 2 (18): 164–165.

Melynias Moore, 1894 (Type species: Papilio lais Cramer, [1777])

Lepidoptera Indica 2 (18): 156–163.

The type species of *Didonis* Hübner was erroneously thought to be *Papilio biblis* Fabricius, 1807 in earlier literature. Scudder (1875) subsequently selected *Papilio vitellia* Stoll as the type species, and this designation thereby prevented misusage of the name and confusion with the genus *Biblis* Fabricius, 1807 as stated by Hemming (1967).

Mimadelias Moore, 1894 (Type species: Elymnias vasudeva Moore, 1858)² Lepidoptera Indica 2 (18): 165–168.

Elymniopsis Fruhstorfer, 1907 (Type species: Papilio phegea Fabricius, 1793)³ Dt. ent. Z. Iris 20 (3): 173–174.

bammakoo-group

bammakoo (Westwood, 1851)

Specimens: Fig. 1A–D; Male Genitalia: Fig. 22A; Distribution: Fig. 27 ssp. bammakoo (Westwood, 1851)

Papilio phegea Fabricius, 1793. **TL**: UGANDA. **TS**: ZMUC. (preoccupied by Papilio phegea Borkhausen, 1788). Ent. Syst. 3 (1): 132.

Melanitis bammakoo Westwood, 1851. **TL:** Ashanti (Ghana: Ashanti Region). **TS:** NHM. Gen. diurn. Lep. 2: 405, pl. 68, fig. 3.

Elymnias phegea var. intermedia Aurivillius, 1898. **TL**: not indicated. **TS**: NRM. K. svenska Vetenskakad. Handl. 31 (5): 45.

Elymnias phegea ab. angustata Bartel, 1905. **TL**: Kamerun, Barombi Station (Cameroon: Southwest Region, Barombi Mbo). **TS**: unknown. Novit. Zool. 12: 129.

Elymiopsis bammakoo var. hybrida Niepelt, 1915. **TL**: Kassai River (Dемоскатіс Republic of Congo: Kasai River). **TS**: NHM. *Int. Ent. Zs.* 9: 58.

Elymniopsis lise Hemming, 1960. TL: UGANDA. TS: ZMUC. (replaced Papilio phegea Fabricius, 1793). Annot. lep. 1: 30.

ssp. rattrayi Sharpe, 1902

Elymnias rattrayi Sharpe, 1902. **TL**: Entebbe (UGANDA: Central Uganda, Entebbe). **TS**: NHM. Entomologist 35: 41.

Elymnias ugandae Grünberg, 1908. **TL**: UGANDA. **TS**: unknown. Sitzungsber. Ges. Naturf. Freunde. Berlin. 1908: 51.

Elymniopsis ugandae f. rattrayi Lewis, 1974. **TL**: UGANDA. **TS**: unknown. Butter-flies of the World, p. 266, pl. 115, fig. 15.

Moore (1894) did not include any species when establishing *Mimadelias* in Part 18 of his *Lepidoptera Indica*. The type species *vasudeva* was subsequently designated as the type species in his Part 19 of the same series.

Elymniopsis has often been regarded as a distinct genus since its establishment in 1907 by Fruhstorfer, and most references of Afrotropical butterflies list it as a genus of its own (e.g., Larsen 2005). Hemming (1943) first synonymized this genus with Elymnias and the opinion was followed by Gardiner (2010) and further supported by the phylogenetic studies by Peña et al. (2006). In our molecular phylogenetic study (Lohman et al. in prep.), this taxon is sister to all of the Asian species. However, aside from their wing patterns, which mimic various Acraea spp. (Nymphalidae: Heliconiinae), the morphological features of this species are not distinct from other Elymnias (Wei et al. in prep.), and we refrain from retaining the monotypic genus Elymniopsis.

Elymniopsis bammakoo rattrayi (Sharpe, 1902). TL: UGANDA. TS: unknown. Butterflies of West Africa, p. 283.

paradoxa-group

paradoxa Staudinger, 1894

Specimens: Fig. 1E-F; Male Genitalia: Fig. 22B; Distribution: Fig. 28

Elymnias paradoxa Staudinger, 1894. TL: Kubary (Рариа New Guinea: Madang Province, Mt. Kubari). TS: ZMHB. Dt. ent. Z. Iris 7 (1): 116.

Elymnias erastus Grose-Smith, 1894. **TL**: Sattelberg (Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg). **TS**: NHM. *Novit. Zool.* 1 (3): 588.

papua-group

papua Wallace, 1869

Specimens: Fig. 1G–M; Male Genitalia: Fig. 22C; Distribution: Fig. 29

ssp. papua Wallace, 1869⁴

Elymnias papua Wallace, 1869. **TL**: New Guinea⁵. **TS:** NHM. Trans. Ent. Soc. Lond. 1869 (4): 329.

Elymnias viridescens Grose-Smith, 1894. **TL**: Humboldt Bay (Indonesia: Papua, Jayapura, Yos Sudarso Bay). **TS**: NHM. Novit. Zool. 1(2): 365, pl. 12, figs 5–6.

Dyctis viridescens var. kakarona Hagen, 1897. **TL**: Sattelberg (Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg). **TS**: NHMT. Jarhb. Nass. Ver. Nat. 50: 78.

Elymnias papua bivittata van Eecke, 1915. **syn. n. TL**: Bivakeiland, Koofbivak, New Guinea (Indonesia: Papua, Asmat Regency, Bivak Island). **TS**: NBC. *Nova Guinea* 13 (1): 65, pl. 3, fig. 5 & 5a.

ssp. lactentia Fruhstorfer, 1907

Elymnias papua lactentia Fruhstorfer, 1907. **TL**: Waigiu Island (Indonesia: West Papua, Raja Ampat Regency, Waigeo). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 240.

ssp. cinereomargo Joicey & Noakes, 1915

Elymnias viridescens cinereomargo Joicey & Noakes, 1915. **TL**: Biak Island (Indonesia: Papua, Biak). **TS**: NHM. Trans. ent. Soc. Lond. 1915 (2): 196.

ssp. climena Talbot, 1932

Elymnias climena Talbot, 1932. **TL**: Mysol Island (Indonesia: West Papua, Raja Ampat Regency, Misool). **TS**: NHM. Bull. Hill Mus. Witley 4 (3): 168.

We recognize 5 subspecies of *papua* in the present study and synonymize *bivitatta* with *papua* because no significant morphological differences were found. In addition, no apparent barriers to dispersal seem to exist between the geographic ranges of these two taxa.

Since Wallace only traveled to the Bird's Head Peninsula on New Guinea, it is likely that the type specimen was collected in what is now the Indonesian province of West Papua.

ssp. euploeoides Talbot, 1932

Elymnias euploeoides Talbot, 1932. **TL**: Batchian (Indonesia: North Maluku, Bacan). **TS**: NHM. Bull. Hill Mus. Witley 4 (3): 167.

esaca-group

esaca (Westwood 1851)⁶

Specimens: Figs 1N–P, 2A–C; Male Genitalia: Fig. 22D–E; Distribution: Fig. 30 ssp. esaca (Westwood, 1851)

Melanitis esaca Westwood, 1851. **TL**: East Indies. **TS**: NHM. Gen. diurn. Lep. 2: 405. Elymnias godferyi Distant, 1883. **TL**: Sungei Ujong (Peninsular Malaysia: Negeri Sembilan, Sungei Ujong). **TS**: NHM. Ann. Mag. nat. Hist. 12 (71): 351.

Dyctis esacoides de Nicéville, [1893]. **TL**: Perak (Peninsular Malaysia: Perak), Battak Mountains⁷ (Indonesia: North Sumatra). **TS**: IM. *J. Bomb. Nat. Hist. Soc.* 7 (3): 323, pl. H, fig. 2.

ssp. egialina (C. & R. Felder, 1863)

Melanitis egialina C. & R. Felder, 1863. **TL**: Luzon (Philippines: Luzon). **TS**: NHMW.

Wien. ent. Monats. 7 (4): 121.

Melanitis ligya C. & R. Felder, 1863. nom. nud. TL: Luzon (Philippines: Luzon). TS: NHMW. Wien. ent. Monats. 7 (4): 121.

Melanitis pallas C. & R. Felder, 1863. nom. nud. TL: Luzon (Philippines: Luzon). TS: NHMW. Wien. ent. Monats. 7 (4): 121.

The distinctiveness of *esaca* and *vasudeva* has never been doubted and they have been treated as distinct species in all prior studies. The former is distributed throughout most of the Greater Sunda Islands, the Philippines, and the Thai-Malay peninsula, and the range of the latter encompasses northeast India, Myanmar, northern Laos, northern Vietnam and southwest China. The wings of male *esaca* are shorter and more attenuate than *vasudeva*, and have black ground coloration with a metallic submarginal band in some specimens. The male of *vasudeva* is not dramatically different from the female in wing shape or color pattern. However, our molecular phylogenetic analysis (Lohman et al. in prep.) reveals that both specimens of *vasudeva* (from China and India) are nested within a clade of three *esaca* specimens from Java, Mindanao, and peninsular Malaysia. This paraphyletic relationship suggests that the two species should be synonymized. However, we regard both species as valid because: 1) wing color and pattern are strongly dimorphic in *esaca*, but more or less monomorphic in *vasudeva*; 2) the wing shape of *esaca* males differs from females, and this is not true of *vasudeva*; and 3) the two taxa are parapatric.

[&]quot;Battak Mountains" is the type locality for many butterfly and other animal taxa, but the name appears on no recent map of Sumatra. It seems to refer to the mountainous region historically inhabited by the Batak ethnic groups in northeast Sumatra. From the description in de Nicéville and Martin (1895), "Battak Mountains" seems to refer to the portion of the Barisan Mountain Range running along the western edge of North Sumatra Province, including the peaks surrounding Lake Toba.

ssp. borneensis Wallace, 18698

Elymnias borneensis Wallace, 1869. **TL**: Sarawak (East Malaysia: Sarawak). **TS**: NHM. Trans. ent. Soc. Lond. 1869 (4): 324.

Elymnias (Mimadelias) esaca taeniola Fruhstorfer, 1907. syn. n. TL: southeast Borneo. TS: NHM. Dt. ent. Z. Iris 20 (3): 250.

ssp. andersonii (Moore, 1886)9

Dyctis andersonii Moore, 1886. TL: Mergui (MYANMAR: Thanintharyi, Mergui Archipelago). TS: NHM. J. Linn. Soc. Lond. 21 (1): 33, pl. 3, fig. 5.

Elymnias (Mimadelias) oberthuri Fruhstorfer, 1902. syn. n. TL: Renong, Siam (Thailand: Ranong). TS: NHM. Soc. Ent. 17 (11): 82.

ssp. maheswara Fruhstorfer, 1894

Elymnias (Dyctis) maheswara Fruhstorfer, 1894. **TL**: Gede Vulcan (Indonesia: West Java, Mt. Gede). **TS**: NHM. Ent. Nachr. 20 (2): 21.

ssp. leontina Fruhstorfer, 1898

Elymnias esaca leontina Fruhstorfer, 1898. **TL**: Nias (Indonesia: North Sumatra, Nias). **TS**: NHM. Ent. Zs. 12 (14): 99.

ssp. pseudodelias Fruhstorfer, 1907

Elymnias (Mimadelias) esaca pseudodelias Fruhstorfer, 1907. **TL**: Sumatra (Indonesia: Sumatra). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 250.

ssp. georgi Fruhstorfer, 1907

Elymnias (Mimadelias) esaca georgi Fruhstorfer, 1907. **TL**: Mindanao (Philippines: Mindanao). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 251.

ssp. saifuli Hanafusa, 1993

Elymnias esaca saifuli Hanafusa, 1993. **TL**: Siberut Island (Indonesia: West Sumatra, Mentawai Islands, Siberut). **TS**: HPC. Futao (11): 3.

ssp. popularis Hanafusa, 1994

Elymnias esaca popularis Hanafusa, 1994. **TL**: Tanahmasa Island (Indonesia: North Sumatra, South Nias Regency, Batu Islands, Tanahmasa). **TS**: HPC. Futao (17): 19.

ssp. splendida Tateishi, 2001

Elymnias esaca splendida Tateishi, 2001. **TL**: Singkep Island (Indonesia: Riau Islands, Lingga Archipelago, Singkep Island). **TS**: FMNH. *Futao* (39): 13.

ssp. lingga Tateishi, 2001

Elymnias esaca lingga Tateishi, 2001. **TL**: Lingga Island (Indonesia: Riau Islands, Lingga Archipelago, Lingga Island). **TS**: FMNH. Futao (39): 14.

The subspecies *esaca taeniola* is synonymized with *esaca borneensis* because there are no consistent morphological differences between them and no obvious biogeographical barriers within the island Borneo that would restrict gene flow and maintain subspecific differences.

oberthuri was originally described as a species by Fruhstorfer (1902b) and subsequently downgraded to be a subspecies of *vasudeva* (Fruhstorfer 1907). We synonymize it with *esaca andersonii* because these two names seem to represent opposite sexes of the same subspecies confined to the Thai-Malay Peninsula.

ssp. nigricans Tateishi, 2001

Elymnias esaca nigricans Tateishi, 2001. **TL**: Enggano Island (Indonesia: Bengkulu, Enggano Island). **TS**: FMNH. Futao (39): 14.

ssp. andrewi Schröder & Treadaway, 2003

Elymnias esaca andrewi Schröder & Treadaway, 2003. **TL**: Philippines: Oriental Mindoro, Mt. Halcon. **TS**: SMFD. Nachr. ent. Ver. Apollo 23 (4): 193, pl. 1, figs 3–4.

ssp. leytensis Schröder & Treadaway, 2003

Elymnias esaca leytensis Schröder & Treadaway, 2003. **TL**: Philippines: Southern Leyte, Saint Bernard, Hinabian. **TS**: SMFD. Nachr. ent. Ver. Apollo 23 (4): 194, pl. 1, figs 7–8.

ssp. tateishii Lamas, 2010

Elymnias esaca tateishii Lamas, 2010. SHILAP 38 (150): 198. (replacement name of Elymnias esaca lautensis Teteishi, 2001).

Elymnias esaca lautensis Tateishi, 2001. **TL**: Laut Island (Indonesia: South Kalimantan, Kota Baru, Laut Island). **TS**: FMNH. Futao (39): 13. (preoccupied by Elymnias harterti lautensis Medicielo & Hanafusa, 1994).

vasudeva Moore, 1857¹⁰

Specimens: Fig. 2D-K; Male Genitalia: Fig. 22F; Distribution: Fig. 31

ssp. vasudeva Moore, 1857

Elymnias (Mimadelias) vasudeva vasudeva Moore, 1857. TL: Darjeeling (India: West Bengal, Darjeeling). TS: NHM. Cat. lep. Ins. Mus. East India Coy. 1: 238.

Elymnias thycana Wallace, 1869. **syn. n. TL**: India. **TS**: NHM. Trans. ent. Soc. Lond. 1869 (4): 323. (8)

Mimadelias deva Moore, 1894. syn. n. TL: Khasia Hills, Assam (India: Meghalaya, Khasi Hills). TS: NHM. Lepid. Ind. 2 (19): 167, pl. 142, fig. 2a.

Mimadelias burmensis Moore, 1893. syn. n. TL: Tenasserim (Myanmar: Tanintharyi, Tenasserim). TS: NHM. Lepid. Ind. 2 (19): 168, pl. 143, fig. 1a–e.

Elymnias vacudera [sic] sinensis Chou, Zhang & Xie, 2000. syn. n. TL: Yunnan (CHINA: Yunnan). TS: NWSUAF. Entomotaxonomia 22 (3): 224, figs 7–8.

dara-group

dara Distant & Pryer, 1887

Specimens: Fig. 3A–D; Male Genitalia: Fig. 22G–I; Distribution: Fig. 32

Having examined all the type specimens and a long series of other material ranging from northeast India to southwest China, we failed to detect any consistent differences among the subspecies described by (Moore 1857; 1894), Wallace (1869), and Chou (2000). We consider all *vasudeva* subspecies to be indistinguishable from one another; the variable wing patterns lack diagnostic differences and are not reliable for delimiting subspecies.

ssp. dara Distant & Pryer, 1887

Elymnias dara Dinstant & Pryer, 1887. **TL**: north Borneo. **TS**: NHM. Ann. Mag. nat. Hist. (5) 19 (109): 50.

ssp. albofasciata Staudinger, 1889

Elymnias albofasciata Staudinger, 1889. **TL**: Philippines: Palawan. **TS**: ZMHB Dt. ent. Z. Iris 2 (1): 39.¹¹

ssp. deminuta Staudinger, 1889

Elymnias albofasciata var. deminuta Staudinger, 1889. **TL**: Lawang (Indonesia: East Java, Malang, Lawang). **TS**: ZMHB. Dt. ent. Z. Iris 2 (1): 40.

ssp. bengena Fruhstorfer, 1907

Elymnias dara bengena Fruhstorfer, 1907. **TL**: Palabuan (Indonesia: West Java, Sukabumi, Pelabuhan Ratu). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 216.

ssp. darina Fruhstorfer, 1907

Elymnias dara darina Fruhstorfer, 1907. **TL**: Battak Mountains (Indonesia: North Sumatra). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 215.

ssp. daedalion (de Nicéville, 1890)

Dyctis daedalion de Nicéville, 1890. **TL**: Myittha (Myanmar: Mandalay, Kyaukse, Myittha). **TS**: IM. *J. Bomb. nat. Hist. Soc.* 5 (3): 202, pl. D, fig. 4.

patna-group

patna (Westwood, 1851)¹²

Specimens: Fig. 3E–I; Male Genitalia: Fig. 22J; Distribution: Fig. 33

Staudinger (1889) described *albofasciata* based on specimens from Palawan. However, the locality of a "type specimen" deposited in ZMHB is labeled as "Tanyong Malim, Malacca". We consider the type to be either mislabeled or simply not a type of this subspecies. Staudinger (1889) indicated that he compared specimens of *dara* from Malacca (specimen provided by Künstler) and Palawan. The mistake in labeling is probably caused by historical confusion of the type locality since its publication.

Moore (1894) described *patnoides* as a distinct species, but Fruhstorfer (1907) downgraded it to be a form of *patna patna*. In the same publication, Fruhstorfer (1907) described *patna stictica* from Vietnamese specimens. Having examined long series from India, Myanmar, northern Thailand, northern Laos, Vietnam and Hainan (China), we find no consistent differences in wing pattern and wing shape among populations in this region. We therefore synonymize both *patnoides* and *stictica* with *patna*. The subspecies *hanitschi* from the Malay Peninsula has slightly different metallic blue sheen from the nominotypical subspecies, and molecular phylogenetic analysis reveals that the *patna* from India and *patna* from Malay Peninsula form distinct sister lineages. We therefore retain the subspecies status of *hanitschi* in the present study. Ek-Amnuay et al. (2007) described *inayoshii* based on specimens collected in Ranong and Trang Provinces in peninsular Thailand. The name, however, is not available under the Code. Additionally, the taxonomic status of the peninsular Thai populations is questionable, as we find that the wing shape and coloration of *inayoshii* are markedly different from *patna patna* and *patna hanitschi*. Since we have no material for DNA sequencing, we cannot determine whether the peninsular Thai populations should be treated as a subspecies of *patna* or a different species altogether. The nomenclatural problem of *inayoshii* requires confirmation of the taxon's species identity.

ssp. patna (Westwood, 1851)

Melanitis patna Westwood, 1851. TL: East India. TS: NHM. Gen. diurn. Lep. 2: 405, pl. 68, fig. 2.

Elymnias patna bercovitzi Joicey & Talbot, 1921. **TL**: Five Finger Mountains (China: Hainan, Wuzhi Mountain). **TS**: NHM. Bull. Hill Mus. Witley 1 (1): 173.

Melanyias patnoides Moore, 1893. syn. n. TL: Burma, Karen Hills, East Pegu (Myanmar: Bago). TS: NHM. Lepid. Ind. 2 (19): 163, pl. 141, fig. 2 & 2a.

Elymnias patna stictica Fruhstorfer, 1902. syn. n. TL: Than-Moi, Nordtonkin (VI-ETNAM: Lang Son, Than Moi). TS: NHM. Dt. ent. Z. Iris 14 (2): 271.

ssp. hanitschi Martin, 1909

Elymnias patna hanitschi Martin, 1909. TL: Malayische Halbinsel (Thai-Malay Peninsula). TS: NHMT. Dt. ent. Z. Iris 22 (1): 52.

peali Wood-Mason, 1883

Specimens: Fig. 3J–K; Male Genitalia: Fig. 22K; Distribution: Fig. 34 *Elymnias peali* Wood-Mason, 1883. **TL**: Aideo, Sibsagar district, Assam (India: Assam, Sivasagar). **TS**: NHM. *Ann. Mag. nat. Hist.* (5) 11: 62, pl. 2, fig. A & B.

ceryx-group

ceryx (Boisduval, 1836)13

Specimens: Fig. 3L–M; Male Genitalia: Fig. 22L; Distribution: Fig. 35

Melanitis ceryx Boisduval, 1836. **TL**: West Java (Indonesia: West Java). **TS**: NHM. Hist. Nat. Ins., Spec. Gén. Lépid. 1: pl. 9, fig. 8.

Elymnias hestinia Fruhstorfer, 1911. **TL**: Java (Indonesia: Java). **TS**: NHM. Gross-Schmett. Erde 9: 383.

kuenstleri Honrath, [1885]

Specimens: Fig. 4A–C; Male Genitalia: Fig. 22M; Distribution: Fig. 36

ssp. kuenstleri Honrath, [1885]

Elymnias künstleri (=kuenstleri) Honrath, [1885]. **TL**: Perak and Malacca (Peninsular Malaysia: Perak and Malacca). **TS**: NHM. Berl. ent. Z. 29 (2): 276, pl. 8, fig. 3.

ssp. gauroides Fruhstorfer, 1894

Elymnias gauroides Fruhstorfer, 1894. TL: Tjisewu, West Java (Indonesia: West

Java, Cisewu). **TS**: NHM. *Ent. Nachr.* 20 (3): 43. ssp. *rileyi* Corbet, 1933

Elymnias kuenstleri rileyi Corbet, 1933. **TL**: Borneo. **TS**: NHM. Stylops 2: 132. Elymnias borneensis Riley, 1923. **TL**: Borneo. **TS**: unknown. Entomologist 56 (717): 36.

Westwood (1851) was possibly unaware of the true collection locality of the type specimen of *ceryx*. Having examined the description, we confirm that the type locality of the type specimen should be Java, not Mexico.

ssp. dobrnii de Nicéville, 189514

Elymnias (Melynias) dohrnii de Nicéville, 1895. **TL**: Bohorok, East Sumatra (Indonesia: North Sumatra, Langkat Regency, Bohorok). **TS**: IM. *J. Bomb. nat. Hist. Soc.* 10 (1): 21, pl. S, fig. 12.

Elymnias kuenstleri mariae Toxopeus, 1936. syn. n. TL: Bekoelen (Indonesia: South Sumatra, Bengkulu). TS: NBC. Ent. Med. Ned. Ind. 2: 46, fig. 1.

ceryxoides de Nicéville, 1895. stat. rev.15

Specimens: Fig. 3N–O; Distribution: Fig. 37

Elymnias (Melynias) ceryxoides de Nicéville, 1895. **TL**: Battak Mountains (Indonesia: North Sumatra). **TS: IM.** J. Bomb. nat. Hist. Soc. 10 (1): 22, pl. S, fig. 13.

Elymnias ceryx ceryxoides f. nigritia Fruhstorfer, 1907. **TL**: Vulkan Singalang (Indonesia: West Sumatra, Agam Regency, Mt. Singgalang). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 213.

pellucida Fruhstorfer, 1895

Specimens: Fig. 4D–E; Male Genitalia: Fig. 22N; Distribution: Fig. 38

Elymnias pellucida Fruhstorfer, 1895. **TL**: Kinabalu (East Malaysia: Sabah, Mt. Kinabalu). **TS**: NHM. Ent. Nachr. 21 (11): 168.

Elymnias annea Pryer & Cator, 1894. TL: Borneo. TS: NHM. Br. N. Borneo Herald 12 (9): 234.

Elymnias aroa Shelford, 1902. **TL**: Mount Penrissen, Sarawak (East Malaysia: Sarawak, Mt. Penrissen). **TS**: SMK. *Proc. Zool. Soc. Lond.* 1902 (2): 272.

penanga-group

penanga (Westwood, 1851)16

Specimens: Fig. 4F-L; Male Genitalia: Fig. 22O; Distribution: Fig. 39

Toxopeus's *mariae* was described from Sumatra, from which de Nicéville's *dohrnii* was also collected. Since there are no remarkable or consistent morphological differences between the subspecies and because no biogeographic or climatic barriers to dispersal seem to exist on Sumatra, we consider *mariae* to be a junior synonym of *dohrnii*. de Nicéville's *dohrnii* was once placed as a subspecies either of *pellucida* (Fruhstorfer 1907) or of *patna* (D'Abrera 1985), here we can confirm it should be associated with *kuenstleri* after having examined the specimens from Sumatra.

The taxonomic status of De Nicéville's *ceryxoides* has been inconsistent. It was originally proposed as a subspecies of *ceryx*, and the treatment was followed by Fruhstorfer (1907). Aoki et al. (1982) suggested upgrading *ceryxoides* as an independent species without giving explanation, but this taxon was again downgraded as a subspecies of *ceryx* by D'Abrera in 1985. Having examined both morphology and genetic data, we conclude that *ceryxoides* should be regarded as a full species endemic to Sumatra.

¹⁶ Elymnias penanga is one of the few Elymnias species with polymorphic female color patterns. However, the female forms are not diagnostically different among subspecies. The diagnostic characters that distinguish subspecies are the size, forewing shape, and metallic sheen of the male.

ssp. penanga (Westwood, 1851)

Melanitis penanga Westwood, 1851. **TL**: Penang (Peninsular Malaysia: Penang). **TS**: NHM. Gen. diurn. Lep. (2): 405.

Melaninis mehida Hewitson, 1863. **TL**: SINGAPORE. **TS**: NHM. *Ill. exot. Butts.* [4] (Melanitis): [69], pl. [36], figs 2–3.

Elymnias abrisa Distant, 1886. **TL**: Province Wellesley (Peninsular Malaysia: Penang, Seberang Perai). **TS**: NHM. Ann. Mag. nat. Hist. 17 (102): 531.

Elymnias penanga penanga f. hislopi (\$\text{\Pi}\$) Eliot, 1967. **TL**: Langkawi (Peninsular Malaysia: Kedah, Langkawi). **TS**: NHM(?). Entomologist 100 (1244): 3.

Elymnias penanga f. immaculata Martin, 1909. **TL**: Indonesia: Sumatra. **TS**: NHMT. Dt. ent. Z. Iris 22 (1): 55.

Elymnias penanga penanga f. johnsoni Talbot, 1929. **TL**: Penang (Peninsular Ma-LAYSIA: Penang). **TS**: NHM. Bull. Hill Mus. Witley 3 (1): 80.

ssp. sumatrana Wallace, 1869

Elymnias sumatrana Wallace, 1869. TL: Sumatra (Indonesia: Sumatra). TS: NHM. Trans. ent. Soc. Lond. 1869 (4): 325.

ssp. konga Grose-Smith, 1889

Elymnias konga Grose-Smith, 1889. **TL**: Kina Balu Mountain, (East MALAYSIA: Sabah, Mt. Kinabalu). **TS**: NHM. Ann. Mag. nat. Hist. (6) 3 (16): 317.

Elymnias borneensis Grose-Smith, 1892. **TL**: Northeast Borneo. **TS**: NHM. Ann. Mag. nat. Hist. (6) 10 (60): 428. (preoccupied by Elymnnias borneensis Wallace 1869)

Elymnias penanga trepsichroides Shelford, 1904. TL: North Borneo. TS: NHM. J. Straits Asiat. Soc. (41): 103. (replacement name for Elymnias borneensis Grose-Smith, 1892)

Elymnias penanga konga f. mehidina, Fruhstorfer, 1907. **TL**: Borneo. **TS**: NHM. Dt. ent. Z. Iris 20 (3): 226.

Elymnias penanga konga f. ptychandrina, Fruhstorfer, 1907. **TL**: North Borneo. **TS**: NHM. Dt. ent. Z. Iris 20 (3): 227.

ssp. chelensis de Nicéville, 1890

Elymnias chelensis de Nicéville, 1890. **TL**: Khasi Hills (India: Meghalaya, Khasi Hills). **TS**: IM. *J. Bomb. nat. Hist. Soc.* 5 (3): 200, pl. D, fig. 3.

hypermnestra-group

hypermnestra (Linnaeus, 1763)

Specimens: Figs 5A–N, 6A–P, 7A–O, 8A–H; Male Genitalia: Fig. 23A–K; Distribution: Fig. 40

ssp. hypermnestra (Linnaeus, 1763)¹⁷

Elymnias hypermnestra is one of the few satyrine species that is regarded as a minor pest of several species of palms. The name has been used numerous times in the taxonomic, ecological, and agricultural literature (Corbet 1943; Koh and Gan 2007; Merrett 1993; Shang-Wen 1998; Yong et al. 2012). However, Lamas (2010) raised concern regarding the validity of this name. This species was originally

- Papilio hypermnestra Linnaeus, 1763. **TL**: Java (Indonesia: Java). **TS**: LSL. Amoenitates Acad. 6: 407.
- Papilio protogenia Cramer, 1779. TL: Java (Indonesia: Java). TS: NBC. Uitl. Kapellen. 2 (16): 141, pl. 189, fig. F-G.
- Hamadryas jynx Hübner, 1808. TL: not indicated. TS: unknown. Erste Zutr. Samml. exot. Schmett. p. 4.
- Elymnias jynx Hübner, 1818. **TL**: East Indies. **TS**: unknown. Zuträge Samml. exot. Schmett. 1: 12.
- Elymnias hypermnestra hypermnestra f. perpusilla Fruhstorfer, 1907. **TL**: Java (Indonesia: Java). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 181.
- Elymnias hypermnestra f. atrata Roepke, 1942. **TL**: Java (Indonesia: Java). **TS**: NBC. Rhop. Javan. (4): 422.¹⁸

placed in *Papilio* by Linnaeus (1763), which made it a junior primary homonym of *Papilio hypermnestra* Scopoli, 1763 (now a synonym of *Zerynthia polyxena* ([Schiffermüller], 1775) (Papilionidae). *Papilio hypermnestra* Linnaeus was published after 23 June 1763, whereas *Papilio hypermnestra* Scopoli was published before that date. Therefore, according the ICZN Article 57.2, both names are primary homonyms and the junior primary homonym (in this case, *hypermnestra* Linnaeus) is permanently invalid (see also Article 23.9.5). Given this set of circumstances, Linnaeus' *hypermnestra* can only be regarded as valid under one of three conditions according to the code:

^{57.2.1.} its use as a valid name (nomen protectum) is maintained under the conditions specified in Article 23.9, or

^{57.2.2.} it is conserved by the Commission under Article 81, or

^{57.2.3.} it, but not its senior homonym, is included in a relevant adopted Part of the List of Available Names in Zoology.."

However, as already stated by Lamas (2010), *hypermnestra* Linnaeus does not fulfill any of the three conditions specified above, because: 1) *hypermnestra* Linnaeus has not been maintained as a nomen protectum and does not fulfill the conditions specified in Article 23.9; 2) *hypermnestra* Linnaeus has not been conserved by the Commission under Article 81; and 3) no part of the List of Available Names in Zoology has been adopted yet for Lepidoptera.

Meanwhile, *hypermnestra* Scopoli has been used numerous times as a valid name after 1899 [see Article 23.9.1.1], and therefore does not qualify as a nomen oblitum. Consequently, if use of the younger homonym [hypermnestra Linnaeus] is to be maintained, the case needs to be submitted to the International Commission for Zoological Nomenclature for a ruling under the plenary power (Article 81). In addition, if Linnaeus's hypermnestra is eventually considered invalid by the Commission, the other earliest available name for this species is Papilio undularis Drury, 1773, which is now used to represent the subspecies of northeast India, and the valid subspecific name for the population of Java would be protogenia Cramer, 1779.

Roepke's *atrata* has rarely been mentioned in previous literature, and, having examined the original description, we regard it as a junior synonym of the nominotypical subspecies, which is also from Java.

ssp. undularis (Drury, 1773)19

Papilio undularis Drury, 1773. **TL**: East Indies. **TS**: NHM. *Ill. Nat. Hist. Exot. Insects* 2: 17, pl. 10, f. 1–2.

Biblis undularis Westwood, 1837. **TL:** East Indies, Java (Indonesia: Java). **TS**: NHM. *Ill. Exo. Ent.* 2: 18, pl. X, figs 1–2.

Melanitis undularis Westwood, 1851. **TL**: East India, Java (Indonesia: Java). **TS**: NHM. Gen. diurn. Lep. 2: 404.

ssp. fraterna Butler, 1871

Elymnias fraterna Butler, 1871. **TL:** Ceylon (SRI LANKA). **TS**: NHM. Proc. Zool. Soc. Lond. 1871: 520, pl. 42, fig. 3.

ssp. nigrescens Butler, 1871

Elymnias nigrescens Butler, 1871. **TL**: Sarawak (East Malaysia: Sarawak). **TS**: NHM. Proc. Zool. Soc. Lond. 1871: 520, pl. 42, fig. 1.

Elymnias hecate Butler, 1871. **TL:** Labuan, Borneo (East Malaysia: Labuan). **TS**: NHM. Proc. Zool. Soc. Lond. 1871 (2): 520, pl. 42, f. 2.

Elymnias nigrescens nigrescens f. pseudagina Fruhstorfer, 1907. **TL:** Sarawak, Borneo (East Malaysia: Sarawak). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 191.

Elymnias nigrescens nigrescens f. edela Fruhstorfer, 1907. **TL:** Pontianak (Indonesia: West Kalimantan, Pontianak). **TS:** NHM. Dt. ent. Z. Iris 20 (3): 191.

Elymnias nigrescens nigrescens f. virilis Fruhstorfer, 1907. **TL:** Lawas (East Malaysia: Sarawak, Lawas). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 191.

Elymnias nigrescens nigrescens f. hecate Fruhstorfer, 1907. **TL:** Labuan (East Malaysia: Labuan). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 191.

ssp. cottonis (Hewitson, 1874). comb. n.20

Melanitis cottonis Hewitson, 1874. **TL:** Andaman Islands (India: Andaman Islands). **TS**: NHM. Ann. Mag. nat. Hist. 14 (83): 358.

Elymnias cottonis Cottonis Fruhstorfer, 1907. TL: Andaman Islands (India: Andaman Islands). TS: NHM. Dt. ent. Z. Iris 20 (3): 183.

Interpretation of the type locality of Drury's *undularis* has been problematic. Drury did not clearly indicate the origin of the specimen he saw but labeled the locality as "East Indies". During the late 18th century, the phrase "East Indies" referred to a wide range of possible localities from India to Indonesia. However, authors working after Drury, without clear reason, interpreted *undularis* as a taxon distributed in northeast India rather than Indonesia. We examined many specimens from north India to Java at different museums and also compared the original drawings of *hypermnestra* (and its junior synonyms) and *undularis* in the literature (*e.g.*, Cramer 1779; Drury 1773), but failed to detect any differences between them. We therefore retain the current concept of *undularis* until more evidence becomes available.

Hewitson's *cottonis* was described as a full species due to the lack of metallic sheen or any other notable markings on the upper side of both the fore- and hindwings; its conspecificity with *hypermnestra* has not previously been suggested. Our unpublished data (Wei et al. in prep.) demonstrates that *cottonis* and *hypermnestra* cannot be distinguished using morphological characters unrelated to possible mimicry, and the molecular phylogeny reveals that cottonis is nested within *hypermnestra* with strong support (Lohman et al. in prep.). We therefore combine *cottonis* (including subspecies *jennifferae* from Little Andaman) with *hypermnestra*, retaining the names *cottonis* and *jennifferae* as distinct subspecies.

ssp. tinctoria Moore, [1879]²¹

Elymnias tinctoria Moore, [1879]. **TL:** Meetan, Moolai (Myanmar: Tanintharyi) **TS**: NHM. *Proc. Zool. Soc. Lond.* 1878 (4): 826.

Elymnias hypermnestra tinctoria f. paraleuca Fruhstorfer, 1907. **TL:** Mergui-Archiel, Tenasserim (Myanmar: Thanintharyi, Mergui Archipelago). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 177.

ssp. hainana Moore, 1878²²

Elymnias hainana Moore, 1878. **TL:** Hainan (China: Hainan). **TS**: NHM. *Proc. zool. Soc. Lond.* 1878 (3): 696.

Elymnias nigrescens formosana Fruhstorfer, 1903. **TL**: Takau (TAIWAN: Kaohsiung). **TS**: NHM. Dt. ent. Z. Iris 16 (1): 17.

Elymnias nigrescens tonkiniana Fruhstorfer, 1902. syn. n. TL: Tonkin, Haiphong (Vietnam: Haiphong). TS: NHM. Dt. ent. Z. Iris 14 (2): 271.

Elymnias hypermnestra nigrescens f. depicta Fruhstorfer, 1907. syn. n. TL: Tonkin (northern Vietnam). TS: NHM. Dt. ent. Z. Iris 20 (3): 188.

Elymnias hypermnestra septentrionalis Chou & Huang, 1994. syn. n. TL: Nanning (China: Guangxi, Nanning). TS: NWSUAF. Monographia Rhopalocerum Sinensium 1: 375, fig. 27.

ssp. discrepans Distant, 1882²³

Elymnias discrepans Distant, 1882. **TL:** Penang, Province Wellesley (Peninsular Malaysia: Penang, Seberang Perai). **TS:** NHM or NHMT. *Ann. Mag. nat. Hist.* (5) 9 (53): 397.

Besides *undularis* from northeast India, there are three other subspecies with orange, *Danaus*-mimicking females distributed in Myanmar, Thailand, and Vietnam. The differences between females of the subspecies *tinctoria*, *violetta*, and *meridionalis*, are subtle. Besides the female form mimicking *Danaus chrysippus* (or *D. genutia*), there is another female form with whitish hindwings (the forms *obfuscata* and *paraleuca*) that possibly mimics either *D. melanippus* or *D. affinis* in Thailand and Vietnam. Since the current subspecies classification has been adopted by local guidebooks and other publications for so long (Corbet et al. 1992; Ek-Amnuay 2012; Monastyrskii 2005; Pinratana 1988), we do not propose any nomenclatural change prior to a thorough phylogenetic/population genetics study based dense sampling of the entire region is completed.

Moore's *hainana* was described from specimens from Hainan Island, China, and the name has been applied to the Taiwanese population since the late 19th century. Since Hainan is between China's Guangxi Province and northern Vietnam, where *septentrionalis* and *tonkiniana* were described, respectively, and because examination of dozens of specimens evince no consistent morphological differences among these subspecies, we synonymize these three names and regard *hainana* as the valid name.

Penang is a small island in the Andaman Sea lying just off the western coast of peninsular Malaysia. The strait that separates this small island (293 km²) from the peninsula is only 2–8 km wide, yet seems to form a dispersal barrier between the peninsular population (commonly known as *agina*, but herein changed to *beatrice*, see discussion below) and insular *discrepans*. The female type specimen of *discrepans* seems to be a morphologically intermediate form between orange, *Danaus*-mimicking *tinctoria* and dark, *Euploea*-mimicking phenotypes. This phenotype has not been documented from the mainland. We therefore retain the name *discrepans* because of the taxon's distinctive female wing patterns; further studies will ascertain whether this subspecies is genetically distinct from other *hypermnestra* subspecies.

ssp. orientalis Röber, 1891

Elymnias orientalis Röber, 1891. **TL**: Flores (Indonesia: East Nusa Tenggara, Flores). **TS**: unknown. *Tijdschr. Ent.* 34: 311.

Elymnias nigrescens dohertyi Fruhstorfer, 1902. **TL**: Ende Island (Indonesia: East Nusa Tenggara, Flores, Ende Island). **TS**: NHM. Dt. ent. Z. Iris 14 (2): 273.

ssp. baliensis Fruhstorfer, 1896

Elymnias protegenia baliensis Fruhstorfer, 1896. **TL**: Bali (Indonesia: Bali). **TS**: NHM. Soc. Ent. 11 (18): 147.

Elymnias nigrescens bulelenga Rothschild, 1915. **TL**: Buleleng (Indonesia: Bali, Buleleng Regency). **TS**: NHM. Novit. Zool. 22 (1): 124.

ssp. violetta Fruhstorfer, 190219

Elymnias undularis violetta Fruhstorfer, 1902. **TL**: Muok-Lek (Thailand: Saraburi, Muak Lek). **TS**: NHM. Soc. Ent. Soc. Ent. 16 (22):169.

Elymnias hypermnestra violetta f. epixantha Fruhstorfer, 1907. **TL**: Bangkok (Тнаг-LAND: Bangkok). **TS:** NHM. Dt. ent. Z. Iris 20 (3):178.

Elymnias hypermnestra violetta f. obfuscata Riley, 1932. **TL**: Siam (THAILAND). **TS:** NHM. J. Siam. Soc. 8 (4, Suppl.): 249.

ssp. meridionalis Fruhstorfer, 190219

Elymnias undularis meridionalis Fruhstorfer, 1902. **TL**: south Annam (southern Vietnam). **TS**: NHM. Soc. Ent. 16 (22): 169.

Elymnias meridionalis f. orphnia, Fruhstorfer, 1907. **TL**: south Annam (southern Vietnam). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 179.

ssp. beatrice Fruhstorfer, 1902. comb. n.24

The taxonomic status and the names applied to the populations of *Elymnias hypermnestra* from Malay Peninsula, Singapore, Borneo, and Sumatra have been historically confusing and chaotic. In 1882, Distant reported and described *nigrescens* from the Malay Peninsula, Malacca, Billiton (Belitung), and Borneo. Since Butler (1871) already stated that the type locality of the "real nigrescens" is Sarawak (Borneo), and the female wing patterns of the populations in Borneo and Malay Peninsula are slightly different, it is not appropriate to apply the name nigrescens to the peninsular population. Fruhstorfer (1902) noticed that "nigrescens" sensu Distant was different from the Bornean one, so he proposed a nomen novum, beatrice, to refer to "nigrescens sensu Distant". The concept of Fruhstorfer's beatrice, however, is probably not monophyletic as he listed Perak, Lingga (Riau), Deli (North Sumatra), and Sumatra in the geographical range of beatrice, but our morphological study does not support lumping the Sumatran population with the peninsular Malaysian one. In the same publication, Fruhstorfer (1902a) described an aberration of nigrescens, namely agina, for populations in Singapore, Sumatra, and Perak. The name agina has been used much more frequently than beatrice to represent the population in the Malay Peninsula including Singapore (Corbet 1943; Lamas 2010; Pinratana 1988). However, Article 45.6.2 of the Code, agina was not an available name when Fruhstorfer first proposed it as an aberrant form of nigrescens (now a valid subspecies of hypermnestra). This name might have subsequently become available by Corbet (1943) when he discussed the taxonomy of the Elymnias hypermnestra of Malay Peninsula, and first used agina to represent the populations in Johor and Singapore. According to the Code (Article 45.5.1), Corbet would be the first author to make agina available so in the present study, we correct the authorship and year of agina to be "Corbet, 1943". Both bea-

Elymnias nigrescens, Distant, 1882. Rhopalocera Malayana: 61.

Elymnias nigrescens beatrice Fruhstorfer, 1902. **nomen n.** for Distant's nigrescens. **TL:** SINGAPORE, Perak (Peninsular Malaysia: Perak), Lingga (Indonesia: Riau Islands, Lingga Archipelago, Lingga Island), Deli, (Indonesia: North Sumatra Province, Deli Serdang Regency), Sumatra (Indonesia: Sumatra), Wellesley Province (Peninsular Malaysia: Penang, Seberang Perai), Billiton (Indonesia: Bangka-Belitung Province, Belitung). **TS:** NHM. Dt. ent. Z. Iris 14 (2): 272.

Elymnias nigrescens ab. agina Fruhstorfer, 1902. **unavailable name. TL**: Singapore, Sumatra (Indonesia: Sumatra), Perak (Peninsular Malaysia: Perak). **TS**: NHM. Dt. ent. Z. Iris 14 (2): 272.²²

Elymnias nigrescens beatrice f. ornamenta Fruhsorfer, 1907. unavailable name. TL: Malay (Peninsular Malaysia). TS: NHM. Dt. ent. Z. Iris 20 (3): 190.²²

Elymnias hypermnestra agina, Corbet, 1943. Proc. Roy. Ent. Soc. Lond. (B) 12: 117–119. ssp. sumbana Fruhstorfer, 1902

Elymnias nigrescens sumbana Fruhstorfer, 1902. TL: Sumba (Indonesia: East Nusa Tenggara, Sumba). TS: NHM. Dt. ent. Z. Iris 14 (2): 273.

ssp. decolorata Fruhstorfer, 1907²⁵

Elymnias nigrescens beatrice forma decolorata Fruhstorfer, 1907. unavailable name.

TL: Sumatra (Indonesia: Sumatra). TS: NHM. Dt. ent. Z. Iris 20 (3): 189.

Elymnias hypermnestra decolorata, Aoki, Yamaguchi & Uémura, 1982. Butterflies of the Southeast Asian Islands 3: 175–176.

ssp. sumbawana Fruhstorfer, 1907

Elymnias nigrescens sumbawana Fruhstorfer, 1907. **TL**: Tambora, Sumbawa (Indonesia: West Nusa Tenggara, Sumbawa, Mt. Tambora). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 197.

trice and agina became available for representing the populations in Malay Peninsula and Singapore. Determination of their validity, therefore, depends on the priority. Considering the fact that Corbet's (1943) use of agina is much later than Fruhstorfer's (1902a) proposal of a nomen novum, we conclude that beatrice should be used to represent the populations in southern part of the Malay Peninsula, including Singapore. The syntype series of both names contain more than one subspecies, so designation of a lectotype for both names will be necessary to fix the concept and use the names. This work will be published elsewhere.

de Nicéville and Martin (1895) stated that they had "great difficulty in identifying satisfactorily the common species of *Elymnias* of the *undularis* group occurring in Sumatra". They decided to follow Distant's (1882a) concept of "*nigrescens*" but still noticed that the Sumatran population of *Elymnias hypermnestra* (as *nigrescens* or *protogenia*) had smaller wings and duller coloration. Fruhstorfer (1907) noticed the opinion of de Nicéville & Martin, and decided to give the Sumatran population a status as a color form, and name it *decolorata*. However, since it was originally published as an infrasubspecific taxon, the name is not available under the Code unless another author uses the name to represent a valid taxon. In 1982, Aoki and colleagues enumerated the subspecies of *Elymnias hypermnestra* that occur throughout its range. They became the first authors to use *decolorata* to represent the Sumatran population. According to the Code (Article 45.5.1), the authorship of *decolorata* should be attributed to Aoki et al. (1982) because they made it available for use for the first time.

ssp. timorensis Fruhstorfer, 1907

Elymnias nigrescens timorensis Fruhstorfer, 1907. **TL**: Timor. **TS**: NHM. Dt. ent. Z. Iris 20 (3): 198.

ssp. alorensis Talbot, 1932

Elymnias nigrescens alorensis Talbot, 1932. **TL**: Alor (Indonesia: East Nusa Tenggara, Alor). **TS**: NHM. Bull. Hill Mus. Witley 4: 167.

ssp. nimota Corbet, 1937

Elymnias hypermnestra nimota Corbet, 1937. **TL**: Tioman (Peninsular Malaysia: Pahang, Rompin, Tioman Island). **TS**: NHM. Proc. R. ent. Soc. Lond. 6 (5): 97.

ssp. kangeana Aoki & Uémura, 1982

Elymnias hypermnestra kangeana Aoki & Uémura, 1982. **TL**: Kangean (Indonesia: East Java, Sumenap Regency, Kangean). **TS**: TPC. Mem. Tsukada Coll. 4: 2.

ssp. robinsona Monastyrskii & Devyatkin, 2003

Elymnias hypermnestra robinsona Monastyrskii & Devyatkin, 2003. **TL**: Con Dao, Con Son Island (Vietnam: Ba Ria–Vung Tau Province, Con Dao Archipelago, Con Son Island). **TS**: NHM. *Atalanta* 34 (1/2): 81, pl. 5, figs 5, 7–8.

ssp. jennifferae Suzuki, 2006. comb. n.

Elymnias cottonis jennifferae Suzuki, 2006. **TL**: Little Andaman (India: Andaman Islands, Little Andaman Island). **TS**: KMSPC. Futao (52): 13.

ssp. uemurai Lamas, 2010 (replaced *Elymnias nigrescens meliophila* Fruhstorfer, 1896a). SHILAP 38 (150): 198.

Elymnias nigrescens meliophila Fruhstorfer, 1896a. **TL**: Lombok (Indonesia: West Nusa Tenggara, Lombok). **TS**: NHM. Soc. Ent.11 (18): 147. (preoccupied by Elymnias hewitsoni meliophila Fruhstorfer 1896b).

caudata Butler, 1871²⁶

Specimens: Fig. 8J–K; Male Genitalia: Fig. 23L; Distribution: Fig. 41 *Elymnias caudata* Butler, 1871. **TL**: Canara (India: Karnataka, Kanara). **TS**: NHM. *Proc. Zool. Soc. Lond.* 1871: 520, pl. 42, fig. 4.

merula Swinhoe, 1915. incertae sedis²⁷

Specimen: Fig. 8K; Distribution: Fig. 42

Elymnias merula Swinhoe, 1915. **TL:** Kandy, Ceylon (Sri Lanka: Central Province, Kandy). **TS**: NHM. Ann. Mag. nat. Hist. 16 (93): 171.

Although *caudata* was originally proposed as a species of its own, some authors (Gupta 2007; Wynter-Blyth 1957) treated it as a subspecies of *hypermnestra* (or *undularis*) due to the similarity in the *Danaus*-mimicking females. Our morphological and molecular studies demonstrate that *caudata* is a distinct, monophyletic taxon that is sister to *hypermnestra*.

Swinhoe's merula is based on a single male type collected from Sri Lanka. Having examined the type deposited in the Natural History Museum, London, we are convinced that merula should be a synonym of hypermnestra. Lamas (pers. comm.) suggests synonymizing merula with the Sri Lankan fraterna; however, the male of Sri Lankan fraterna is quite different from merula and we cannot at present conclude that synonymizing it with this subspecies is warranted. We presume that the single specimen of merula was accidentally introduced with imported palms or is an aberration; we treat this name as incertae sedis.

leucocyma Godart, 1819. incertae sedis²⁸

DISTRIBUTION: Fig. 43

Biblis leucocyma Godart, 1819. **TL:** Java (Indonesia: Java). **TS**: unknown. Encyc. Méth. 9: 326.

nepheronides-group

nepheronides Fruhstorfer, 1907²⁹

Specimens: Fig. 8L–N; Male Genitalia: Fig. 23M; Distribution: Fig. 44 ssp. nepheronides Fruhstoerfer, 1907

Elymnias nepheronides Fruhstorfer, 1907. **TL**: Flores Island (Indonesia: East Nusa Tenggara, Flores). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 228.

Elymnias detanii Aoki & Uémura, 1982. TL: Flores (Indonesia: East Nusa Tenggara, Flores). TS: NODAI. Butterflies of the Southeast Asian Islands 3: 208.

ssp. tamborana Okubo, 2010

Elymnias tamborana Okubo, 2010. **TL**: Mt. Ngegep, Sumbawa (Indonesia: West Nusa Tenggara, Sumbawa, Mt. Sengenges). **TS**: OPC. *Trans. Lep. Soc. Jpn.* 60 (4): 255–257.

harterti-group

harterti Honrath, 188930

Specimens: Fig. 9A–F; Distribution: Fig. 45

The true identity of Godart's *leucocyma* has been problematic since its description in 1819. Godart specified "Java" as the source of the specimen but gave a vague description without any figure. Doubleday (1844) suggested that northern India (near the border with Myanmar) might be the source of the specimen. Moore (1878a) mentioned the name *leucocyma* in his checklist without providing any further information. In 1882, Marshall & de Nicéville recognized the validity of *leucocyma* and synonymized *malelas* with it. However, Moore (1894) considered *leucocyma* to be the name that should be validated rather *malelas*. Fruhstorfer (1907), based on Godart's simple description, doubted that the origin of specimen was Java or northern India, and suggested placing *leucocyma* closer to *hypermnestra*. There are more than 2 species with color patterns similar to *leucocyma* (viz. forewing with metallic blue sheen and hindwing with undulate margin) in Java and northern India, so we cannot specify the use of this name until more evidence becomes available. Moreover, Hewitson's figure (1861: pl. 9, fig. 34) of *leucocyma* was a misidentification of *hewitsoni* and has no relevance to this problem.

Our molecular phylogenetic analysis confirms that *detanii* and *nepheronides* represent opposite sexes of the same species as Araya (2016) demonstrated using morphology. We also accept Araya's (2016) decision to include *tamborana* as a subspecies of *nepheronides* on morphological grounds; we currently have no genetic data from *tamborana*.

Having examined specimens deposited in the NHM, we are confident that *harterti* and *brookei* should be regarded as different subspecies of the same species. Moulton's *smithi* is identical to Shelford's *brookei* so they are synonymized in the present study.

ssp. harterti Honrath, 1889

Elymnias harterti Honrath, 1889. **TL**: Perak (Peninsular Malaysia: Perak). **TS**: NHM. Berl. ent. Z. 33 (1): 165.

ssp. brookei Shelford, 1904

Elymnias brookei Shelford, 1904. TL: Sarawak (East Malaysia: Sarawak). TS: NHM. J. Straits Asiat. Soc. (41): 102.

Elymnias smithi Moulton, 1915. syn. n. TL: Mt. Molu (East Malaysia: Sarawak, Mt. Molu). TS: NHM. Entomologist 48: 98.

ssp. lautensis Medicielo & Hanafusa, 1994

Elymnias harterti lautensis Medicielo & Hanafusa, 1994. **TL**: Laut Island (Indonesia: South Kalimantan, Kota Baru Regency, Laut Island). **TS**: HPC. Futao (15): 17, pl. 4, figs 17–18.

ssp. arbaimuni Hanfusa, 2005

Elymnias haterti [sic] arbaimuni Hanfusa, 2005. **TL:** Indonesia: Jambi Province, Kuala Tungkal, Suban. **TS**: HPC. Futao (49): 11, pl. 1, figs 11–12.

parce Staudinger, 1889

Specimens: Fig. 9G–J; Male Genitalia: Fig. 23N; Distribution: Fig. 46 ssp. parce Staudinger, 1889³¹

Elymnias panthera parce Saudinger, 1889. **TL**: Palawan (Philippines: Palawan). **TS**: ZMHB. *Dt. ent. Z. Iris* 2 (1): 39.

ssp. justini Schröder & Treadaway, 2003

Elymnias parce justini Schröder & Treadaway, 2003. **TL**: Philippines: Palawan, Busuanga Island. **TS**: SMFD. Nachr. ent. Ver. Apollo 23 (4): 194, pl. 1, fig. 21.

panthera-group

panthera (Fabricius, 1787)

Specimens: Figs 9K, 10A–P; Male Genitalia: Figs 23O, 24A; Distribution: Fig. 47 ssp. panthera (Fabricius, 1787)³²

Papilio panthera Fabricius, 1787. TL: Tranquebariae (India: Tamil Nadu, Tharangambadi). TS: ZMUC. Mantissa Ins. 2: 39.

Staudinger (1889) placed *parce* as a subspecies of *panthera*, but morphological and molecular evidence suggest that *parce* does not belong to the *panthera*-group; it is more closely allied to *harterti*.

Fabricius stated that the type locality of the nominotypical *panthera* is Tranquebar (Tharangambadi, Tamil Nadu) in southern India, but the current distribution of this species in India seems to be restricted to the north. It is necessary to confirm the actual distribution of the species in India to verify whether the type locality falls in the actual distribution range or is simply a port from which the specimen was exported during the colonial period.

ssp. *dusara* (Horsfield, [1829])³³

Melanitis dusara Horsfield, [1829]. **TL**: West Java (Indonesia: West Java). **TS**: NHM. Descr. Cat. lep. Ins. Mus. East India Coy. 2: pl. 5, f. 7.

ssp. mimus Wood-Mason & de Nicéville, 1881

Elymnias mimus Wood-Mason & de Nicéville, 1881. **TL**: Nicobar Islands (India: Nicobar Islands). **TS**: uknown. *J. Asiat. Soc. Bengal* 50: 230.

ssp. dolorosa Butler, 1883.

Elymnias dolorosa Butler, 1883. TL: Nias Island (Indonesia: North Sumatra, Indonesia, Nias). TS: NHM. Ent. mon. Mag. 20: 53.

ssp. lutescens Butler, 1867. comb. n., stat. n.³⁴

Elymnias lutescens Butler, 1867. **TL**: Malacca, Singapore and Penang (SINGAPORE & Peninsular Malaysia: Penang and Malacca). **TS**: NHM. *Ann. Mag. nat. Hist.* 20 (120): 404, pl. 9, f. 10.

Elymnias panthera var. labuana Staudinger, 1889. **syn. n. TL**: Labuan Island (East Malaysia: Labuan). **TS**: ZMHB. *Dt. ent. Z. Iris* 2 (1): 39.

Elymnias panthera lacrima Fruhstorfer, 1904. **syn. n. TL**: [North Borneo], [Banka] (Indonesia: Banka-Belitung Province, Banka Island). **TS**: NHM. *Berl. ent. Zs.* 49: 188.

Elymnias defasciata Fruhstorfer, 1911, syn. n. TL: Borneo. TS: TS: NHM. Gross-Schmett. Erde 9: 372.

Elymnias panthera alfredi Fruhstorfer, 1907. syn. n. TL: Southeast Borneo. TS: NHM. Dt. ent. Z. Iris 20 (3): 220.

Elymnias panthera alfredi f. pantherina Fruhstorfer, 1907. unavailable name. TL: Southeast Borneo. TS: NHM. Dt. ent. Z. Iris 20 (3): 220.

Elymnias panthera alfredi f. alfredi Fruhstorfer, 1907. unavailable name. TL: Southeast Borneo. TS: NHM. Dt. ent. Z. Iris 20 (3): 220.

ssp. enganica Doherty, 1891

Elymnias enganica Doherty, 1891. **TL**: Engano (Indonesia: Bengkulu, Enggano Island). **TS**: NHM. J. Asiat. Soc. Bengal. Part 2, 60 (1): 24.

The subspecies *dusara* and *dulcibella* were both described from Java, suggesting the names might be synonymous. However, many lepidopteran species have distinctive populations western and eastern parts of the island (Aoki et al. 1982; Tsukada and Nishiyama 1982; Yata and Morishita 1985), and we therefore retain these two subspecies as valid.

Butler's *lutescens* was proposed as a full species based on specimens from Borneo (collected by Lowe), Malacca, Singapore, and Penang (from Roberts' collection), and according to Butler (1867: 404), *lutescens* was similar to *dusara*. This taxon, however, has been synonymized with the Indian nominotypical subspecies for long with no clear reason. In the present study, we revalidate the name and use it to represent the population in Borneo, as Borneo is the first locality mentioned in Butler's original description. The other conspecific taxa described from Borneo, such as *labuana*, *lacrima*, *defasciata*, *alfredi*, and *pantherina* are therefore newly synonymized with *lutescens* in the present study. It is not clear whether *panthera* from peninsular Malaysia is genetically distinct from Bornean populations, so we do not further revise the plethora of subspecific names associated with *panthera*.

ssp. lacrimosa Fruhstorfer, 1898

Elymnias panthera lacrimosa Fruhstorfer, 1898. **TL**: Bawean Island (Indonesia: East Java, Gresik Regency, Bawean). **TS**: NHM. Berl. ent. Zs. 43: 196.

ssp. suluana Fruhstorfer, 1899

Elymnais panthera suluana Fruhstorfer, 1899. **TL**: Sulu Island (Philippines: Sulu Province, Sulu Island). **TS**: NHM. Berl. ent. Zs. 44: 57.

ssp. bangueyana Fruhstorfer, 1899

Elymnias panthera bangueyana Fruhstorfer, 1899. **TL**: Banguey Island (MALAYSIA: Sabah, Banggi Island). **TS**: NHM. Berl. ent. Zs. 44: 58.

ssp. dulcibella Fruhstorfer, 1907

Elymnias panthera f. dulcibella Fruhstorfer, 1907. **TL**: East Java (Indonesia: East Java). **TS**: NHM Dt. ent. Z. Iris 20 (3): 223.³¹

ssp. tautra Fruhstorfer, 1907

Elymnias panthera tautra Fruhstorfer, 1907. **TL**: Northeast Sumatra (Indonesia: North Sumatra). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 218 (repl. *E. lutescens* Martin & de Nicéville, 1896)

ssp. arikata Fruhstorfer, 1907

Elymnias panthera arikata Fruhstorfer, 1907. **TL**: Natuna Island (Indonesia: Riau Province, Natuna Island). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 219.

ssp. balina Martin, 1909

Elymnias panthera balina Martin, 1909. **TL**: Bali Island (Indonesia: Bali). **TS**: NHMT. Dt. ent. Z. Iris 22 (1): 58.

ssp. exsulata van Eecke, 1918

Elymnias panthera exsulata van Eecke, 1918. **TL**: Pulu [sic] Lasia (Indonesia: North Sumatra, Lasia Island). **TS**: NBC. Zoologische Mededeelingen 4 (2): 82.

ssp. winkleri Kalis, 1933

Elymnias panthera winkleri Kalis, 1933. **TL**: Sabang, Weh Island (Indonesia: Aceh, Sabang, Weh Island). **TS**: MEPR. *Tijdschrift voor Entomologie* 76 (1–2): 80.

ssp. mira Corbet, 1942

Elymnias panthera mira Corbet, 1942. **TL**: Sipora Island (Indonesia: West Sumatra, Mentawai Regency, Sipora). **TS**: NHM. Ann. Mag. nat. Hist. (11) 9 (56): 612.

ssp. tiomanica Eliot, 1978

Elymnias panthera tiomanica Eliot, 1978. **TL**: Tioman (Peninsular Malaysia: Pahang, Rompin, Tioman Island). **TS**: NHM. Butterflies of the Malay Peninsula, 3rd ed: 413.

ssp. belitungensis Okano, 1986

Elymnias panthera belitungensis Okano, 1986. **TL**: Belitung Island (Indonesia: Bangka-Belitung Province, Belitung). **TS**: OMPC. *Tokurana* 11 (1): 1, figs 1–6.

ssp. ruricolaris Hanafusa, 1989

Elymnias panthera ruricolaris Hanafusa, 1989. **TL**: Karimata Island (Indonesia: West Kalimatan Province, Karimata Island). **TS**: HPC. Futao (3): 10, pl. 3, figs 1—4.

ssp. banyakensis Hanafusa, 1993

Elymnias panthera banyakensis Hanafusa, 1993. **TL**: Kepulauan Banyak (Indonesia: Aceh, Banyak Islands). **TS**: HPC. Futao (13): 8.

ssp. attenuata Hanafusa, 1994

Elymnias panthera attenuata Hanafusa, 1994. **TL**: Tanahmasa Island (Indonesia: North Sumatra Province, Tanahmasa Island). **TS:** HPC. Futao (4): 13.

ssp. redangensis Hanafusa, 2001

Elymnias panthera redangensis Hanafusa, 2001. **TL**: Redang Island (Peninsular Malaysia: Terengganu, Redang Island). **TS**: HPC. Futao (37): 14, pl.1, figs 5–8.

ssp. zeta Abang, Treadaway & Schröder, 2004

Elymnias panthera zeta Abang, Treadaway & Schröder, 2004. **TL**: Balambangan Island (East Malaysia: Sabah, Balambangan Island). **TS**: MUS. Futao (47): 10, pl. 3, figs 33–36.

obnubila Marshall & de Nicéville, 1883

Specimens: Fig. 11A–B; Male Genitalia: Fig. 24B; Distribution: Fig. 48

Elymnias obnubila Marshall & de Nicéville, 1883. **TL**: Mergui (Myanmar: Than-intharyi, Mergui Archipelago). **TS**: IM. Butts India Burmah Ceylon 1 (2): 272.

congruens Semper, 1887

Specimens: Fig. 11C–G; Male Genitalia: Fig. 24C; Distribution: Fig. 49 ssp. congruens Semper, 1887³⁵

Elymnias congruens Semper, 1887. **TL:** N. Mindanao (Philippines: northern Mindanao). **TS:** SMFD. *Reisen. Philipp.* 2: 61, pl. 11, fig. 8–10.

Elymnias congruens photinus Fruhstorfer, 1907. syn. n. TL: N. Mindanao (Philippines: northern Mindanao). TS: NHM. Dt. ent. Z. Iris 20 (3): 199.

Elymnias congruens phaios Fruhstorfer, 1907. syn. n. TL: S. Mindanao (Philippines: southern Mindanao). TS: NHM. Dt. ent. Z. Iris 20 (3): 200.

Elymnias congruens rafaela Fruhstorfer, 1907. syn. n. TL: Bazilan (Philippines: Sulu Archipelago, Basilan). TS: NHM. Dt. ent. Z. Iris 20 (3): 200.

ssp. subcongruens Semper, 1892

Elymnias subcongruens Semper, 1892. **TL:** Mindoro (Philippines: Mindoro). **TS:** SMFD. Reisen. Philipp. 7: 329.

ssp. endida Fruhstorfer, 1911

Elymnias congruens endida Fruhstorfer, 1911. **TL:** Bohol (Philippines: Bohol). **TS:** NHM. *Gross-Schmett. Erde* 9: 379.

Having examined the type material described by Fruhstorder and Semper, we are convinced that only one subspecies of *congruens* is distributed on the island Mindanao, and therefore synonymize *photinus*, *phaios*, and *rafaela* with the nominotypical *congruens*.

ssp. salipi Schroeder & Treadaway, 1989

Elymnias salipi Schroeder & Treadaway, 1989. **TL:** Philippines: Tawi-Tawi Archipelago, Sanga Sanga Island, Boloboc. **TS**: SMFD. Ent. Z. 99 (22): 327, fig. 6.

ssp. jekei Schroeder & Treadaway, 1989

Elymnias jekei Schroeder & Treadaway, 1989. **TL:** Philippines: Luzon, Nueva Ecija, near Carranglan. **TS:** SMFD. Ent. Z. 99 (22): 328, fig. 6.

ssp. neergaardorum Schroeder & Treadaway, 2003

Elymnias neergaardorum Schroeder & Treadaway, 2003. **TL:** PHILLIPINES: Masbate. **TS**: SMFD. Nachr. ent. Ver. Apollo 23 (4): 194, pl. 1, figs 14–15.

miyagawai Saito & Kishi, 2012

Specimens: Fig. 11H–I; Distribution: Fig. 50

Elymnias miyagawai Saito & Kishi, 2012. **TL**: VIETNAM: Lam Dong. **TS**: SPC. Butterflies (62): 4, figs 1–2, 10.

nesaea-group

nesaea (Linnaeus, 1764)

Specimens: Fig. 12A–O; Male Genitalia: Fig. 24D–G; Distribution: Fig. 51 ssp. nesaea (Linnaeus, 1764)³⁶

Papilio (Nymphalis) nesaea Linnaeus, 1764. **TL:** [Java] (Indonesia: Java). **TS:** LSL. Mus. Lud. Ulr. Reg.: 302.

Papilio lais Cramer, 1777. **TL:** Java (Indonesia: Java). **TS:** unknown. *Uitl. Kapellen* 2 (10): 21, pl. 110, f. A–B.

Elymnias nesaea hermia Fruhstorfer, 1907. syn. n. TL: near Lawang, (Indonesia: East Java, Lawang). TS: NHM. Dt. ent. Z. Iris 20 (3): 206.³⁴

ssp. timandra Wallace, 186937

Elymnias timandra Wallace, 1869. **TL:** Sylhet (Bangladesh: Sylhet Division), Moulmein (Myanmar: Mon State, Mawlamyine). **TS:** NHM. *Trans. ent. Soc. Lond.* 1869 (4): 326.

Elymnias nesaea cortona Fruhstorfer, 1911. syn. n. TL: Burma (Myanmar). TS: NHM. Gross-Schmett. Erde 9: 379.

ssp. laisidis de Nicéville, 1896

Elymnias (Melynias) laisidis de Nicéville, 1896. **TL:** Sumatra (Indonesia: Sumatra). **TS:** IM. J. Asiat. Soc. Bengal, Part 2, 64 (3): 390.

Linnaeus did not indicate from which part of Java his specimen of *nesaea* was collected, and we found no consistent differences among Javan *nesaea* populations based on examination of specimens at several different museums, so we combine Fruhstorfer's *hermia* with the nominotypical *nesaea*.

Wallace's *timandra* from Sylhet, Bangladesh, is not different from Fruhstorfer's *cortona* from Myanmar, so we synonymize them.

ssp. baweana Hagen, 1896

Elymnias baweana Hagen, 1896. **TL:** Bawean Island (Indonesia: East Java, Gresik, Bawean). **TS:** NHMT. *Jahrb. Nass. Nat.* 49: 184, pl. 4, fig. 6.

ssp. neolais de Nicéville, 1898

Elymnias (Melynias) neolais de Nicéville, 1898. **TL:** Nias Island (Indonesia: North Sumatra, Nias). **TS:** IM. *J. Bomb. nat. Hist. Soc.* 12 (1): 136, pl. X, fig. 6.

ssp. apelles Fruhstorfer, 1902

Elymnias lais apelles Fruhstorfer, 1902. TL: Bangkok (THAILAND: Bangkok). TS: NHM. Soc. Ent. 16 (22): 169

ssp. vordemani Snellen van Vollenhoven, 1902

Elymnias vordemani Snellen van Vollenhoven, 1902. **TL:** Kangean Island (Indonesia: East Java, Sumenap, Kangean). **TS:** NBC. *Tijdschr. Ent.* 45: 77, pl. 8, fig. 1.

ssp. hypereides Fruhstorfer, 1903 36

Elymnias lais hypereides Fruhstorfer, 1903. **TL:** North Borneo. **TS:** NHM. Dt. ent. Z. Iris 15 (2): 315

Elymnias nesaea coelifrons Fruhstorfer, 1907. syn. n. TL: Southeast Borneo (Indonesia: South or East Kalimantan). TS: NHM. Dt. ent. Z. Iris 20 (3): 205.38

ssp. kamarina Fruhstorfer, 1906

Elymnias lais kamarina Fruhstorfer, 1906. **TL:** Batu Island (Indonesia: North Sumatra, South Nias Regency, Batu Islands). **TS:** NHM. Ent Zs. 20 (15): 98.

ssp. lioneli Fruhstorfer, 1907

Elymnias nesaea lioneli Fruhstorfer, 1907. **TL:** MALAYSIA. **TS:** NHM. Dt. ent. Z. Iris 20 (3): 203.

ssp. tawicola Schröder & Treadaway, 1989

Elymnias nesaea tawicola Schröder & Treadaway, 1989. **TL:** Philippines: Tawi-Tawi Archipelago, Sibutu Island, Cavan Cavan. **TS:** SMFD. *Ent. Z.* 99 (22): 326, fig. 4.

casiphone Geyer, [1827]

Specimens: Fig. 12A–M; Male Genitalia: Fig. 24H–L; Distribution: Fig. 52 ssp. casiphone Geyer, [1827]

Elymnias casiphone Geyer, [1827]. **TL:** not indicated. **TS**: unknown. *Samml. exot. Schmett.* 3: pl. [9], f. 1–2.^{39,40}

We examined many *nesaea* from different regions of Borneo and found no consistent difference among them. Frustorfer's *coelifrons* is therefore treated as a junior synonym of *hypereides*. The relationship between the Malayan *lioneli* with *hypereides* can be addressed in future phylogenetic studies.

Lamas (pers. comm.) regards *casiphone* and *kamara* as different species, so *erinyes*, *exclusa*, and *lombokiana* are therefore regarded as subspecies of *kamara*. Our phylogenetic study based on morphology and DNA sequence data, however, show that *kamara* is conspecific with *casiphone*; *kamara* seems to represent a sexually dimorphic, mimetic form in which both males and females differ from the sexually dimorphic mimetic forms of *casiphone*. We therefore associate all subspecies previously included under *kamara* with *casiphone*.

⁴⁰ Geyer, when describing *casiphone*, did not specify the geographical provenance of his specimen. Westwood (1851) and Fruhstorfer (1907) suspected that Java was possibly the origin of Geyer's *casiphone*.

Elymnias kamara Moore, [1858]. syn. n. TL: Java (Indonesia: Java). TS: NHM. Cat. lep. Ins. Mus. East India Coy 1: 239.

Elymnias kamara pareuploea Fruhstorfer, 1911. **TL:** [Java] (Indonesia: Java). **TS**: NHM. Gross-Schmett. Erde 9: 382, pl. 87e.

Elymnias kamara pseudalumna Fruhstorfer, 1911. **TL:** Java (Indonesia: Java). **TS:** NHM. Gross-Schmett. Erde 9: 382.

ssp. erinyes de Nicéville, 1895. comb. rev.41

Elymnias (Melynias) erinyes de Nicéville, 1895. **TL:** Battak Mountains (Indonesia: North Sumatra). **TS**: IM. J. Bomb. nat. Hist. Soc. 10 (1): 19, pl. R, figs 9–10.

ssp. praetextata Fruhstorfer, 1896

Elymnias casiphone praetextata Fruhstorfer, 1896. **TL:** Lombok (Indonesia: West Nusa Tenggara, Lombok). **TS**: NHM. Soc. Ent. 11 (17): 140.⁴²

Elymnias kamara lombokiana Fruhstorfer, 1911. syn. n. TL: Lombok Island (Indonesia: West Nusa Tenggara, Lombok). TS: NHM. *Gross-Schmett. Erde* 9: 383.³⁸ ssp. exclusa de Nicéville, 1898. comb. n.

Elymnias (Melynias) exclusa de Nicéville, 1898. **TL:** Bali (Indonesia: Bali). **TS**: IM. J. Asiat. Soc. Bengal, Part II 66 (4): 681.⁴³

Elymnias casiphone djilantik Martin, 1909, **syn. n. TL:** Bali (Indonesia: Bali). **TS**: NHMT. Dt. ent. Z. Iris 22 (1): 49.⁴¹

ssp. alumna Fruhstorfer, 1907

Elymnias casiphone alumna Fruhstorfer, 1907. **TL:** East Java (Indonesia: East Java). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 209.

malelas (Hewitson, 1863)44

Specimens: Fig. 14A–D; Male Genitalia: Fig. 24M; Distribution: Fig. 53 ssp. malelas (Hewitson, 1863)

Melanitis malelas Hewitson, 1863. **TL:** East India. **TS**: NHM. *Ill. exot. Butts.* 4: [70], pl. [36], f. 6–7.

Elymnias malelas malelas ab. subdecorata Fruhstorfer, 1911. unavailable name. TL: Assam (India: Meghalaya). TS: NHM. Gross-Schmett. Erde 9: 381.

Elymnias malelas ivena Fruhstorfer, 1911. syn. n. TL: THAILAND, N. VIETNAM. TS: NHM. Gross-Schmett. Erde 9: 381.

Having compared the original drawing of *casiphone* and the specimens from Java, Sumatra, Bali and Lombok, we conclude that the color pattern of the Javanese population matches well with Geyer's figure.

de Nicéville's *erinyes* was originally described as a full species, and then downgraded to be a subspecies of *casiphone* by Fruhstorfer (1907) or *kamara* (Corbet et al. 1992). Since we now consider this subspecies should be associated with *casiphone*, Fruhstorfer's combination should be revived.

Since we regard *kamara* as a junior synonym of *casiphone*, the name *lombokiana*, originally described as a subspecies of *kamara*, is treated as a new junior synonym of *praetextata* in the present study.

⁴³ Martin's *djilantik* and de Nicéville's *exclusa* were previously placed under *casiphone* and *kamara*, respectively. We regard them as different color forms.

We examined many specimens from northeast India to Vietnam and found no consistent morphological differences to support the current subspecies classification. We therefore synonymize *ivena* and *nilamba* with *malelas*.

Elymnias malelas nilamba Fruhstorfer, 1911. syn. n. TL: INDIA. TS: NHM. Gross-Schmett. Erde 9: 381.

saueri Distant, 188245

Specimens: Fig. 14E–F; Distribution: Fig. 54

ssp. saueri Distant, 1882

Elymnias saueri Distant, 1882. **TL:** Malaysia, Province Wellesley (Peninsular Malaysia: Penang, Seberang Perai). **TS:** NHM. *Rhopalocera Malayana* p. 65, pl. 9, fig. 3.

kochi Semper, 1887⁴⁶

Specimens: Fig. 14G–H; Male Genitalia: Fig. 24N; Distribution: Fig. 55

ssp. kochi Semper, 1887

Elymnias kochi Semper, 1887. TL: PHILIPPINES: Central Luzon. TS: SMFD. Reisen Philipp. (2) 55: 63, pl. 12, fig. 4.

casiphonides Semper, 189247

Specimens: Fig. 14I–J; Male Genitalia: Fig. 24O; Distribution: Fig. 56

ssp. casiphonides Semper, 1892

Elymnias casiphonides Semper, 1892. **TL:** PHILIPPINES: Mindanao. **TS:** SMFD. Reisen Philipp. (7): 330.

ssp. sanrafaela Schröder & Treadaway, 1980

Elymnias casiphonides sanrafaela Schröder & Treadaway, 1980. **TL:** PHILIPPINES: Samar, San Rafael **TS:** SMFD. Ent. Z. 90 (21): 238, fig. 3.

nelsoni Corbet, 1942

Specimens: Fig. 14K–L; Male Genitalia: Fig. 25A; Distribution: Fig. 57

ssp. nelsoni Corbet, 1942

Elymnias nelsoni Corbet, 1942. **TL**: Mentawei Islands (Indonesia: West Sumatra, Mentawai Islands). **TS:** NHM. Ann. Mag. nat. Hist. (11) 9 (56): 612, fig. 5.

amoena Tsukada & Nishiyama, 1979

Specimens: Fig. 14M; Distribution: Fig. 58

Distant's *saueri* was originally described as a full species and then placed under *casiphone* as a subspecies by Fruhstorfer (1907) due to the similarity in wing pattern. Recently, Araya and Saito (2014) separated them into two morphologically defined species. Our phylogenetic analysis reveals that these taxa are not even sister to each other. The sister species of *saueri* is *saola*, and we therefore affirm the species status of *saueri*.

Semper (1887) described *kochi* as a full species, while Fruhstorfer downgraded it to be a subspecies of *beza* due to the similarity of their wing patterns. Treadaway and Schroeder (2012) considered *kochi* a full species, and our phylogenetic study places *kochi* as the sister group of *kanekoi* from Negros, so its status as a full species is upheld.

The physiognomy of *casiphonides* is remarkably similar to female *casiphone* and female *malelas*, however, our molecular phylogenetic study places it as the sister group of *nesaea*. The similarity is almost certainly the result of these different lineages mimicking the same widespread model: female *Euploea mulciber*.

ssp. amoena Tsukada & Nishiyama, 1979

Elymnias amoena Tsukada & Nishiyama, 1979. **TL**: Sumba (Indonesia: East Nusa Tenggara, Sumba). **TS:** TPC. Mem. Tsukada Coll. 1: 15, figs 19–20.

kanekoi Tsukada & Nishiyama, 1980

Specimens: Fig. 14N–O; Male Genitalia: Fig. 25B; Distribution: Fig. 59

ssp. kanekoi Tsukada & Nishiyama, 1980

Elymnias kanekoi Tsukada & Nishiyama, 1980. **TL**: north Negros (Рніціррімеs: Negros Occidental). **TS:** TPC. Mem. Tsukada Coll. 2: 14, f. 8–9, 14

saola Monastyrskii, 2004

Specimens: Fig. 14P; Distribution: Fig. 60

ssp. saola Monastyrskii, 2004

Elymnias saola Monastyrskii, 2004. TL: VIETNAM: Nghe An Province, Pu Mat Nature Reserve. TS: NHM. Atalanta 35 (1/2): 45, pl. 2a, figs 1–2; fig. 1A, 3

melias-group

melias (C. & R. Felder, 1863)48

Specimens: Fig. 15A–D; Male Genitalia: Fig. 25C; Distribution: Fig. 61 ssp. melias (C. & R. Felder, 1863)

Melanitis melias C. & R. Felder, 1863. **TL**: Lugban (Philippines: Luzon, Quezon, Lucban) and Burias Island (Philippines: Masbate, Burias Island). **TS**: NHMW. Wien. ent. Monats. 7 (4): 120.

ssp. malis Semper, 1887

Elymnias melias malis Semper, 1887. TL: Casiguran (Philippines: Central Luzon, Aurora, Casiguran). TS: SMFD. Reisen Philipp. (2): 62, pl. 12, figs 2–3.

Elymnias palmifolia Schultze, 1908. **TL:** Cagayang (Рнігіррімеs: Northern Luzon, Cagayan). **TS:** ECMP. *Philipp. J. Sci* 3 (1): 27, pl. 1, fig. 1.

beza (Hewitson, 1877)

Specimens: Fig. 15E–F; Male Genitalia: Fig. 25D; Distribution: Fig. 62.

ssp. beza (Hewitson, 1877)

Melanitis beza Hewitson, 1877. **TL**: Philippines: Mindanao. **TS**: NHM. Ent. Mon. Mag. 13: 179.

⁴⁸ According to the current taxonomy, two subspecies of *melias* are recognized and distributed in Luzon, and it seems unusual for a single island to harbor more than one subspecies. The biotic regions of Luzon, however, are complex. The northern Sierra Madre mountains may serve as a geographical barrier within the island as suggested by Vallejo (2014).

Elymnias kochi plateni Fruhstorfer, 1907. syn. n. TL: Philippines: Mindanao. TS: NHM. Dt. ent. Z. Iris 20 (3): 228.⁴⁹

ssp. samarana Schröder & Treadaway, 1980

Elymnias beza samarana Schröder & Treadaway, 1980. **TL**: Philippines: Samar, San Rafael. **TS**: SMFD. Ent. Z. 90 (21): 236, fig. 2.

sansoni Jumalon, 1975

Specimens: Fig. 15G–J; Male Genitalia: Fig. 25E; Distribution: Fig. 63

ssp. sansoni Jumalon, 1975

Elymnias sansoni Jumalon, 1975. TL: PHILIPPINES: Negros. TS: JPC. Trans. Lep. Soc. Jpn. 26 (2): 47.

ssp. aklanensis Uémura & Kitamura, 2001

Elymnias sansoni aklanensis Uémura & Kitamura, 2001. **TL**: Philippines: Panay, Aklan Province, Makato, Castillo. **TS**: TME. Butterflies 29: 5.

luteofasciata Okubo, 1980

Specimens: Fig. 15K–L; Distribution: Fig. 64

Elymnias luteofasciata Okubo, 1980. **TL:** Philippines: Mindanao, Davao, Penangudloton, Upian River, Calinan. TS: OPC. *Tyô to Ga* 31 (1,2): 60.

vitellia-group

vitellia (Stoll, [1781])

Specimens: Fig. 15M–P; Male Genitalia: Fig. 25F–G; Distribution: Fig. 65 ssp. vitellia (Stoll, [1781])

Papilio vitellia Stoll, [1781]. **TL**: Ambon (Indonesia: Maluku, Ambon). **TS**: unknown. *Uitl. Kapellen.* 4 (30): 116, pl. 349, fig. E–F.

Melanitis stellaris Snellen van Vollenhoven, 1861. **TL**: [New Guinea]. **TS**: NBC. Tijdschr. Ent. 4 (5/6): 159, pl. 8, fig. 3.

Elymnias vitellia f. basium Fruhstorfer, 1907. **unavailable name. TL**: Saparua (Indonesia: Maluku, Saparau). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 230.

Elymnias vitellia ceramensis Martin, 1909. **TL**: Ceram (Indonesia: Maluku, Seram). **TS**: NHMT. Dt. ent. Z. Iris 22 (1): 65.

ssp. viminalis Wallace, 1869

Elymnias viminalis Wallace, 1869. TL: Buru Island (Indonesia: Maluku, Buru). TS: NHM. Trans. ent. Soc. Lond. 1869 (4): 328.

⁴⁹ Fruhstorfer (1907) placed *plateni* as a subspecies of *kochi*, but our molecular phylogenetic analysis reveals that *kochi* is the sister species of *kanekoi*. Therefore, *plateni* should be synonymized with the nominotypical *beza*, which is a member of the *melias* group.

agondas (Boisduval, 1832)50

Specimens: Figs 16A–H, 17A–I, 18A–M, 19A–M; Male Genitalia: Fig. 25H–N; Distribution: Fig. 66

ssp. agondas (Boisduval, 1832)⁵¹

Dyctis agondas Boisduval, 1832. **TL**: Vanikoro (Solomon Islands: Temotu Province, Vanikoro). **TS**: unknown. *Voy. Astrolabe*. 1: 138.

Dyctis bioculatus Westwood, 1851. syn. n. TL: Arfak Mountains (Indonesia: West Papua). TS: NHM. Gen. diurn. Lep. 2: 354, pl. 54, fig. 4.

Elymnias agondas muscosa Fruhstorfer, 1907. **TL:** Kapaur (Indonesia: West Papua, Fakfak). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 243.

Elymnias agondas tampyra Fruhstorfer, 1907. **TL**: Kumusi River (Papua New Guinea: Northern Province, Kumusi River). **TS**: NHM. Ent. Rundschau 31 (5): 25.

Elymnias agondas hagias Fruhstorfer, 1914. **TL**: Eilandenfluß (Indonesia: Papua, Pulau River). **TS**: NHM. Ent. Rundschau 31 (5): 25

ssp. melane (Hewitson, 1858)

Melanitis melane Hewitson, 1858. TL: [Key Island] (Indonesia: Maluku, Kei Island). TS: NHM. Proc. zool. Soc. Lond. 1858: 465, pl. 55, figs 2, 4.

Elymnias (Dyctis) mela de Nicéville, 1902. TL: Key Island (Indonesia: Maluku, Kei Island). TS: IM. J. Bomb. nat. Hist. Soc. 14 (2): 238, pl. FF, figs 4–5.

Elymnias (Dyctis) meletus de Nicéville, 1902. **TL**: Key Island (Indonesia: Maluku, Kei Island). **TS**: IM. J. Bomb. nat. Hist. Soc. 14 (2): 241.

Elymnias (Dyctis) melitia de Nicéville, 1902. **TL**: Key Island (Indonesia: Maluku, Kei Island). **TS**: IM. J. Bomb. nat. Hist. Soc. 14 (2): 242.

ssp. melantho Wallace, 1869

Elymnias melantho Wallace, 1869. **TL**: Gagie Island (Indonesia: West Papua, Raja Ampat Regency, Gag Island). **TS**: NHM. *Trans. ent. Soc. Lond.* 1869 (4): 330.

The species *agondas* has long been considered a highly variable species, the females of which mimic various *Taenaris* spp. throughout its range in New Guinea and the surrounding islands. Our phylogenetic analysis, however, reveals that *thryallis*, which was currently placed as a subspecies of *cybele*, is nested within *agondas*, and the branch support for this relationship is strong. We therefore conclude that both *agondas* and *cybele* are not monophyletic species as currently circumscribed. We sink *thryallis* into *agondas*, thus forming a monophyletic species, but further clarification of the subspecific nomenclature is difficult because of the myriad described taxa, vague descriptions of many type localities (frequently "New Guinea"), and our lack of access to material of several rare "subspecies" of *agondas*, *cybele*, and other members of the species group.

The true identity of *agondas* is mysterious. Boisduval stated that the source of the type specimen was the Solomon Islands (Boisduval 1832: 138, pl. 3, fig. 5). However, no *Elymnias* are known from the Solomon Islands at present (Tennent 2002), and the easternmost point in the range of this species is Woodlark Island in Milne Bay Province, Papua New Guinea—approximately 350 km from the Solomon Islands across the Solomon Sea. Although the circumscription of "Solomon Islands" has changed throughout history, an area with that name has never included Woodlark Island. Bougainville Island can be included in the Solomon Islands, but *Elymnias agondas* has never been found there. The original drawing of *agondas* is a male, and since the highly variable wing pattern of male *agondas* is not a reliable diagnostic character, we tentatively retain the nominotypical *agondas* as a taxon with questionable geographical provenance, but the nominal subspecies should not be applied to any population until the true collection locality of the type can be discerned.

Elymnias agondas moranda Fruhstorfer, 1904. **TL**: Waigeu (Indonesia: West Papua, Raja Ampat Regency, Waigeo). **TS**: NHM. Dt. ent. Z. Iris 16 (2): 322.

ssp. glaucopis Staudinger, 1894

Elymnias glaucopis Staudinger, 1894. **TL**: Sattelberg (Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg). **TS**: ZMHB. *Dt. ent. Z. Iris* 7 (1): 116.

Elymnias agondas glaucopis Fruhsforfer, 1907. TL: New Guinea. TS: NHM. Dt. ent. Z. Iris 20 (3): 243.

ssp. melanippe Grose-Smith, 1894

Elymnias melanippe Grose-Smith, 1894. **TL**: Sattelberg (Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg). **TS**: NHM. Novit. Zool. 1 (3): 587.

Elymnias vertenteni Hulstaert, 1925. TL: Irian Jaya (Indonesia: Papua or West Papua). TS: NBC. Ann. Mag. nat. Hist. (9) 15 (88): 447.

ssp. melanthes Grose-Smith & Kirby, 1897

Elymnias melanthes Grose-Smith & Kirby, 1897. **TL**: Woodlark Island (Papua New Guinea: Milne Bay, Woodlark Island). **TS**: NHM. Ann. Mag. nat. Hist. (6) 19: 178.

Elymnias agondas melanthes f. *infernalis* (♀) Fruhstorfer, 1914. **TL**: Not indicated. **TS**: NHM. *Ent. Rundschau* 31 (5): 26.

Elymnias agondas melanthes f. *virginalis* (♀) Fruhstorfer, 1914. **TL**: Not indicated. **TS**: NHM. *Ent. Rundschau* 31 (5): 26.

ssp. melagondas Fruhstorfer, 1900

Elymnias melagondas Fruhstorfer, 1900. **TL**: New Guinea. **TS**: NHM. Stett. ent. Ztg. 60 (10-12): 339.

Elymnias agondas melagondas f. taenarides (\$\top\$) Fruhstorfer, 1914. **TL**: Milnebai (Рариа New Guinea: Milne Bay). **TS**: NHM. Ent. Rundschau. 31 (5): 26.

ssp. australiana Fruhstorfer, 1900

Elymnias australiana Fruhstorfer, 1900. **TL**: Cape York (Australia: Queensland, Cape York). **TS**: NHM. Stett. ent. Ztg. 60 (10-12): 339.

ssp. aruana Fruhstorfer, 1900

Elymnias aruana Fruhstorfer, 1900. **TL**: Aru (Indonesia: Maluku, Indonesia). **TS**: NHM. Stett. ent. Ztg. 60 (10-12): 341.

ssp. goramensis Fruhstorfer, 1900

Elymnias goramensis Fruhstorfer, 1900. **TL**: Goram Island (Indonesia: Maluku, East Seram Regency, Gorong Island). **TS**: NHM. Stett. ent. Ztg. 60 (10-12): 341.

ssp. agondina Fruhstorfer, 1904

Elymnias agondina Fruhstorfer, 1904. **TL**: Salewatti (Indonesia: West Papua, Raja Ampat Islands, Salawati). **TS**: NHM. Dt. ent. Z. Iris 16 (2): 322.

ssp. dampierensis Rothschild, 1915

Elymnias dampierensis Rothschild, 1915. TL: Dampier (Papua New Guinea: Madang, Karkar Island). TS: NHMT. Novit. Zool. 22 (2): 201.

ssp. multocellata van Eecke, 1915

Elymnias multocellata van Eecke, 1915. **TL**: Kloofbivak (Indonesia: Papua). **TS**: NBC. Nova Guinea 13 (1): 66, pl. 3, f. 6.

ssp. thryallis Kirsch, 1876. comb. n.48

- Elymnias thryallis Kirsch, 1876. **TL**: Mysore, Kordo (Indonesia: Papua, Biak). **TS**: SMTD. *Mitt. zool. Mus. Dresden* 1: 119, pl. 6, fig. 4.
- Elymnias glauconia Staudinger, 1894. **TL**: Kubary (Papua New Guinea: Jiwaka, Mt. Kubari). **TS:** ZMHB. *Dt. ent. Z. Iris* 6 (2): 362, pl. 6, fig. 2.
- Elymnias glauconia var. chloera Staudinger, 1894. **TL**: New Guinea. **TS**: ZMHB. Dt. ent. Z. Iris 6 (2): 363.
- Elymnias thryallis f. brunnescens Fruhstorfer, 1911. **TL**: New Guinea. **TS**: NHM. Gross-Schmett. Erde 9: 389.
- Elymnias thryallis f. pseudosalpinx Fruhstorfer, 1911. **TL**: New Guinea. **TS**: NHM. Gross-Schmett. Erde 9: 389.
- Elymnias thryallis f. terentilina Fruhstorfer, 1911. **TL**: New Guinea. **TS**: NHM. Gross-Schmett. Erde 9: 389.
- Elymnias thryallis f. violacea Fruhstorfer, 1911. **TL**: Waigiu Island (Indonesia: West Papua, Raja Ampat Regency, Waigeo). **TS**: NHM. *Gross-Schmett. Erde* 9: 389.

cybele (C. & R. Felder, 1860)

Specimens: Fig. 20A–F; Male Genitalia: Figs 25O, 26A; Distribution: Fig. 67 ssp. cybele (C. & R. Felder, 1860)⁵²

- Melanitis cybele C. & R. Felder, 1860. TL: Batschian Island (Indonesia: North Maluku, Bacan). TS: NHMW. Wien. ent. Monats. 4 (8): 248.
- Dyctis astrifera Butler, 1874. TL: Batchian (Indonesia: North Maluku, Bacan). TS: NHM. Trans. ent. Soc. Lond. 1874 (4): 425.
- Elymnias cybele opaca Fruhstorfer, 1907. syn. n. TL: Halmaheira (Indonesia: North Maluku, Halmahera). TS: NHM. Dt. ent. Z. Iris 20 (3): 229.
- Elymnias cybele ternatana syn. n. Fruhstorfer, 1907. TL: Ternate (Indonesia: North Maluku, Ternate). TS: NHM. Dt. ent. Z. Iris 20 (3): 229.

ssp. obiana Fruhstorfer, 1904

Elymnias obiana Fruhstorfer, 1904. **TL**: Obi Island (Indonesia: North Maluku, Obi). **TS**: NHM. *Dt. ent. Z. Iris* 16 (2): 321.

ssp. adumbrata Fruhstorfer, 1907. subsp. rev.53

Elymnias cybele adumbrata Fruhstorfer, 1907. **TL**: Buru (Indonesia: Maluku, Buru). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 228.

Our phylogenetic analysis shows that *cybele cybele* from Bacan is nested within *cybele opaca* from Halmahera. Morphological examination failed to distinguish these two subspecies; we therefore synonymize them.

The subspecies *adumbrata* was described from Buru, but it was synonymized with the nominotypical *cybele* by previous authors. Since the wing pattern of *adumbrata* is different from that of *cybele*, and Buru island is presently ~280 km from Halmahera, we revive this subspecies from synonymy with *cybele cybele*.

cumaea (C. & R. Felder, [1867])⁵⁴

Specimens: Fig. 20G–H; Male Genitalia: Fig. 26B; Distribution: Fig. 68 ssp. cumaea (C. & R. Felder, [1867])⁵⁵

Melanitis cumaea C. & R. Felder, [1867]. **TL**: Halmahera (Indonesia: North Maluku Halmahera). **TS**: NHMW. Reise. Fregatte. Novara. 2 (3): 452, pl. 452., pl. 61, f. 9–10.

ssp. thyone Fruhstorfer, 1904. comb. n., stat. n.56

Elymnias thyone Fruhstorfer, 1904. **TL**: [North Celebes] (Indonesia: North Sulawesi, Indonesia). **TS**: NHM. Soc. Ent. 19: 53.

ssp. toliana Fruhstorfer, 189957

Elymnias cumaea toliana Fruhstorfer, 1899. **TL**: Toli Toli (Indonesia: Central Sulawesi, Tolitoli). **TS**: NHM. Berl. Ent. Zs. 44 (1/2): 53.

Elymnias pseudeuploea Fruhstorfer, 1911. **unavailable name. TL**: Sulawesi (Indonesia: Sulawesi). **TS**: NHM. *Gross-Schmett. Erde* 9: 385.

hewitsoni Wallace, 1869

Specimens: Fig. 20I–J; Male Genitalia: Fig. 26C; Distribution: Fig. 69

ssp. hewitsoni Wallace, 1869

Elymnias hewitsoni Wallace, 1869. TL: Macassar (Indonesia: South Sulawesi, Makassar). TS: NHM. Trans. ent. Soc. Lond. 1869 (4): 327.

Elymnias hewitsoni hewitsoni f. sumptuosa Fruhstorfer, 1907. **TL**: Tanetta (Indonesia: Central Sulawesi, Poso Regency, Tentena). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 237.

ssp. meliophila Fruhstorfer, 1896

Elymnias meliophila Fruhstorfer, 1896. **TL**: Saleyer (Indonesia: South Sulawesi, Selayar Islands, Selayar). **TS**: NHM. Soc. Ent. 11 (4): 25.

ssp. atys Fruhstorfer, 1904

Elymnias hewitsoni atys Fruhstorfer, 1904. **TL**: Bouthain, south Celebes (Indonesia: South Sulawesi, Moncong Lompobatang). **TS**: NHM. Soc. Ent. 19 (8): 60.

According to our phylogenetic analysis, *cumaea* is not a monophyletic group and is part of a radiation on Sulawesi that includes *hicetas* and *hewitsoni*. The subspecies *phrikonis* is not allied with other *cumaea* subspecies, but comprises the sister group to a clade including *cybele*, *vitellia*, *holofernes* and *agondas*. We therefore elevate *phrikonis* to the species level. Fruhstorfer (1907) described *relicina* from Sanana (Sula Besi), and we consider this name should be synonymized with *phrikonis* as they are not different from each other morphologically.

Nominotypical *cumaea* is only reported from Halmahera. We have not been able to obtain specimens for inclusion in the molecular phylogeny so we have no indication of how many subspecies previously associated with *cumaea* should be retained.

Having examined specimens of *thyone*, we conclude that this taxon should not be regarded as a junior synonym of *cumaea cumaea*, but we tentatively place *thyone* as a subspecies of *cumaea* pending molecular data for inclusion in a phylogenetic study.

In our phylogenetic study, a specimen from North Sulawesi identified as *toliana* is sister to *hicetas*, and this pair is sister to *bornemanni*, which we regard as a full species. Since we have no genetic data from nominotypical *cumaea*, we are unsure were to place this taxon and tentatively retain *toliana* as a subspecies of *cumaea*, even though this arrangement makes *cumaea* polyphyletic.

mimalon (Hewitson, 1861)

Specimens: Fig. 20K–N; Male Genitalia: Fig. 26D; Distribution: Fig. 70

ssp. mimalon (Hewitson, 1861)

Melanitis mimalon (Hewitson, 1861). **TL**: Toli-Toli (Indonesia: Central Sulawesi, Tolitoli). **TS**: NHM. *Proc. zool. Soc. Lond.* 1861: 52, pl. 9, figs 1–2.

Elymnias mimalon mimalon f. leucostigmata Fruhstorfer, 1907. **TL**: Toli-Toli (Indonesia: Central Sulawesi, Tolitoli). **TS**: NHM. Dt. ent. Z. Iris 20 (3): 239.

ssp. ino Fruhstorfer, 1904

Elymnias mimalon ino Fruhstorfer, 1904. **TL**: Tawaya, Celebes (Indonesia: Central Sulawesi, Towaya). **TS**: NHM. Soc. Ent. 19 (7): 53.

ssp. nysa Fruhstorfer, 1907

Elymnias mimalon nysa Fruhstorfer, 1907. **TL**: South Celebes (Indonesia: Southeast Sulawesi). **TS**: NHM. *Dt. ent. Z. Iris* 20 (3): 239, pl. 7, fig. 5.

hicetas Wallace, 1869

Specimens: Fig. 20O-P; Male Genitalia: Figs 26E-F; Distribution: Fig. 71

ssp. hicetas Wallace, 1869

Elymnias hicetas Wallace, 1869. **TL**: Macassar, south Celebes (Indonesia: South Sulawesi, Makassar). **TS**: NHM. Trans. ent. Soc. Lond. 1869 (4): 327.

Elymnias hicetas bonthainensis Fruhstorfer, 1899. syn. n. TL: Bua Kraeng (Indonesia: South Sulawesi, Mt. Bawakaraeng). TS: NHM. Berl. ent. Zs. 44 (1/2): 55.58

ssp. hicetina Fruhstorfer, 1904

Elymnias hicetas hicetina Fruhstorfer, 1904. **TL**: Tombugu (Indonesia: Central Sulawesi, Tombuko). **TS**: NHM. Soc. Ent. 19 (7): 53.

ssp. butona Fruhstorfer, 1904

Elymnais hicetas butona Fruhstorfer, 1904. TL: North Buton (Indonesia: Southeast Sulawesi, Buton). TS: NHM. Soc. Ent. 19 (7): 53.

ssp. rarior Martin, 1929⁵⁹

Elymnias hicetas rarior Martin, 1929. **TL**: Celebes (Indonesia: Sulawesi). **TS**: NHMT. Mitt. münchn. ent. Ges. 19: 160.

holofernes (Butler, 1882)

Specimens: Fig. 21A–B; Male Genitalia: Fig. 26G; Distribution: Fig. 72

Dyctis holofernes Butler, 1882. TL: Duke-of-York Island (Papua New Guinea: East New Britain, Duke of York Island). TS: NHM. Ann. Mag. nat. Hist. 10

(55): 42.

Having examined the type specimens of *bonthainensis* and *hicetas*, we failed to find any distinguishing morphological characters. These two names are therefore synonymized.

Martin described *rarior* as a subspecies of *hicetas* without a clear indication of its type locality in Sulawesi. In our phylogenetic study, two specimens identified as *rarior* are paraphyletic with regard to *hicetas* and *butona*. Since the type locality of *rarior* is unclear, we retain *rarior* as a subspecies of *hicetas*.

bornemanni Ribbe, 1889. stat. n.60

Specimens: Fig. 21C–D; Male Genitalia: Fig. 26H; Distribution: Fig. 73 *Elymnias bornemanni* Ribbe, 1889. **TL**: Bangkai (Indonesia: Central Sulawesi, Banggai). **TS**: SMTD (?). *Dt. ent. Z. Iris* 2 (1): 183, pl. 3, f. 1–2.

phrikonis Fruhstorfer, 1899. stat. n.61

Specimens: Fig. 21E–F; Male Genitalia: Fig. 26I; Distribution: Fig. 74

Elymnias cumaea phrikonis Fruhstorfer, 1899. **TL**: Sula Besi and Sula-Mangoli

(Indonesia: North Maluku, Sula Islands, Sanana and Mangole). **TS**: NHM.

Berl. ent. Zs. 44 (1/2): 53.

Elymnias cumaea relicina Fruhstorfer, 1907. syn. n. TL: Sula Besi (Indonesia: North Maluku, Sula Islands, Sanana). TS: NHM. Dt. ent. Z. Iris 20 (3): 234.

sangira Fruhstorfer, 1899

Specimens: Fig. 21G–H; Male Genitalia: Fig. 26J; Distribution: Fig. 75

Elymnias cumaea sangira Fruhstorfer, 1899. **TL**: Sangir, Sulawesi (Indonesia: North Sulawesi, Sangihe Islands, Sangir Besar). **TS**: NHM. Berl. ent. Zs. 44 (1/2): 54.

umbratilis Joicey & Noakes, 1915. stat. n.62

Specimens: Fig. 21I–J; Male Genitalia: Fig. 26K; Distribution: Fig. 76

Elymnias cybele umbratilis Joicey & Noakes, 1915. **TL**: Biak (Indonesia: Papua, Biak). **TS**: NHM. Trans. ent. Soc. Lond. 1915 (2): 195.

resplendens Martin, 1929. stat. n.63

Specimens: Fig. 21K–L; Male Genitalia: Fig. 26L; Distribution: Fig. 77

Elymnias cumaea resplendens Martin, 1929. **TL**: Celebes (Indonesia: Sulawesi). **TS**: NHMT. Mitt. münchn. ent. Ges. 19: 162.

The situation of *bornemanni* is similar to that of *phrikonis*. It is not closely related to other *cumaea* subspecies, so we treat it as a full species.

⁶¹ phrikonis has been regarded as a subspecies of cumaea. Our phylogenetic analysis, however, places it as the sister to a clade consisting of cybele, holofernes, umbratilis, vitellia, and agondas. We therefore elevate phrikonis to full species status. Since relicina was described from the same locality as phrikonis we synonymize these two names in the present study.

⁶² Elymnias cybele umbratilis was originally described based on five syntypes from Biak and synonymized with thryallis by subsequent authors. Our phylogenetic analysis, however, reveals that umbratilis is a distinct taxon, not closely related to any subspecies of cybele, and sister to holofernes. We therefore revive this taxon and give it full species status.

Martin (1929) placed *resplendens* with *cumaea*, but our analysis suggests that *resplendens* is closely related to *hewitsoni* and deserves full species status.

Species not placed in any group⁶⁴

singhala Moore, [1875]

Specimens: Fig. 21M–N; Male Genitalia: Fig. 26M; Distribution: Fig. 78

Elymnias singhala Moore, [1875]. TL: Colombo, Ceylon (Sri Lanka: Western Province, Colombo). TS: NHM. Proc. zool. Soc. Lond. 1874 (4): 568.

Discussion

Wing patterns of *Elymnias* butterflies appear to be highly evolvable, which facilitates Batesian mimetic resemblance to a variety of phenotypically dissimilar model species. Many *Elymnias* are found on islands in the Indo-Australian Archipelago, and the isolation provided by islands seems to provide the opportunity for divergence and local adaptation, facilitating resemblance to different model species in different locales. The remarkable capacity for phenotypic evolution of wing patterns has resulted in sexually dimorphic mimicry, convergence of distantly related taxa on similar wing patterns, and marked phenotypic divergence among conspecific popuations. These phenomena have previously confounded attempts to produce an accurate taxonomic framework because few if any morphological characters are taxonomically or phylogenetically informative. Wing veination, male genitalia, and female genitalia are remarkably uniform among species of *Elymnias*; only slight variation in male genitalia might be useful for discriminating some species. Species delimitation and diagnosis in *Elymnias* has therefore traditionally relied almost entirely on wing patterns. Our molecular phylogeny, which uses genetic markers presumed to be unrelated to wing phenotypes, has detected multiple instances of similar wing patterns in non-sister Elymnias lineages that mimic the same, widespread model species. This similarity seems to be the result of convergent evolution, and we have therefore split these taxa into two or more monophyletic lineages (e.g., E. cumaea and E. cybele have each been split into four and three different species, respectively). On the other hand, some Elymnias species—like other mimetic butterfly taxa (Kunte et al. 2014; Merrill et al. 2015; Thompson and Timmermans 2014)—are polymorphic, with single species expressing different mimetic phenotypes in allopatric populations where they mimic different models. We have identified several instances of one nominal species nested within another, and synonymize these taxa under a single species name (e.g., E. cottonis into E. hypermnestra and E. cybele thryallis into E. agondas).

Strong dimorphism caused many early workers to describe males and females as separate species, most of which have been synonymized. In this paper we confirmed

We have been unable to obtain DNA sequence data from our tissue samples of *singhala* from old museum specimens. This species is probably not closely related to either the *hypermnestra* or *harterti* species group, but its true species group affinity cannot be deduced at this time.

Araya's (2016) conclusion of synonymizing *E. detanii*, known only from males, into *E. nepheronides*, known only from females; this rare species is known only from the Indonesian islands of Flores and Sumbawa. Similarly, *E. vasudeva oberthurii* has been sunk into *E. esaca andersonii*, as these apparently represent different sexes of the same species.

Females of several *Elymias* species, including *E. agondas*, *E. hypermnestra*, and *E. esaca*, are morphologically variable across their range. Rather than recognize every wing pattern variant as a different subspecies, we have synonymized many subspecies into geographically cohesive taxa, for example, within the islands of Borneo or New Guinea.

Much of the mismatch between Elymnias' previous taxonomic framework and its evolutionary history is due to rapid evolutionary change. This resulted in morphologically-delimited nominal species that were polyphyletic. In these cases, our molecular phylogenetic results make delimiting species relatively straightforward. However, there are several cases that are not as clear-cut. For example, we elected to retain E. esaca and E. vasudeva as distinct species despite their paraphyletic relationship because of marked, species-specific morphological differences in these two parapatrically distributed taxa. Population genetic theory predicts incomplete lineage sorting of genetic loci to persist for some time after speciation, resulting in paraphyletic species; the probability of reciprocal monophyly increases with time since divergence (Avise and Ball 1990). Thus, requiring all species to be monophyletic would underestimate true species diversity (Hickerson et al. 2006), particularly in recently diverged species (Knowles and Carstens 2007) such as esaca and vasudeva. However, we decided to sink E. kamara into E. casiphone despite their morphological differences because both taxa are wholly sympatric and because morphologically intermediate specimens are known. We included four specimens of E. c. casiphone and four of E. "kamara" from Java, Bali, and Lombok in our molecular phylogeny, and the topology of all genetic loci individually and together clearly indicated these taxa were conspecific. We suspect that a genetic switch is responsible for the distinct pair of E. casiphone casiphone male and female phenotypes (which mimic Euploea mulciber males and females) and the different, sexually dimorphic forms of E. casiphone kamara, which mimic other Euploea species.

Our molecular phylogeny identifies several examples of allopatrically or parapatrically distributed populations that form distinct, monophyletic sister groups: *E. sansoni sansoni* on Negros and *E. sansoni aklanensis* on Panay; *E. patna* from India and *E. patna* from peninsular Malaysia; *E. vitellia vitellia* from Seram and *E. vitellia viminalis* from Buru; and *E. hypermnestra* from Java and the Lesser Sundas and *E. hypermnestra* from everywhere else. These monophyletic sister lineages would likely be considered different species under a strict phylogenetic species concept, and, in most cases, preliminary Bayesian species delimitation analyses with the program Bayesian Phylogenetics and Phylogeography (BPP; Yang and Rannala 2010) suggest the sister lineages are different species. However, we refrain from splitting these species because we regard the geographic sampling of our phylogenetic work as too sparse, consider the degree of phylogenetic distance between the lineages to be too small, or otherwise fail to find convincing evidence that

reciprocal monophyly is the result of anything more than geographical isolation. In addition, a recent simulation study suggests that programs such as BPP delimit population structure, not species (Sukumaran and Knowles 2017). Further work may find convincing evidence to split one or more of these pairs into two species.

Although there is one African and several mainland Asian species, most of *Elymnias*' diversity is found on the islands of the Indo-Australian Archipelago. Islands are considered laboratories for the study of evolution because they promote isolation and divergence while simplifying the task of delimitating populations and other taxa. Evolutionary study of this taxon provides an excellent opportunity to study the role of archipelagoes in diversification, and the evolutionary genetics of evolutionary novelty and speciation.

List of taxonomic changes

New synonyms

Elymnias papua bivittata van Eecke, 1915, of Elymnias papua papua Wallace, 1869 Elymnias (Mimadelias) esaca taeniola Fruhstorfer, 1907, of Elymnias esaca borneensis, Wallace, 1869

Elymnias (Mimadelias) oberthuri Fruhstorfer, 1902, of Elymnias esaca andersonii (Moore, 1886)

Elymnias thycana Wallace, 1869, of Elymnias vasudeva vasudeva Moore, 1857

Mimadelias deva Moore, 1894, of Elymnias vasudeva vasudeva Moore, 1857

Mimadelias burmensis Moore, 1893, of Elymnias vasudeva vasudeva Moore, 1857

Elymnias vacudera [sic] sinensis Chou, Zhang & Xie, 2000, of Elymnias vasudeva vasudeva Moore, 1857

Melanyias patnoides Moore, 1893, of Elymnias patna patna (Westwood, 1851)

Elymnias patna stictica Fruhstorfer, 1902, of Elymnias patna patna (Westwood, 1851)

Elymnias kuenstleri mariae Toxopeus, 1936, of Elymnias kuenstleri Honrath, [1885]

Elymnias nigrescens tonkiniana Fruhstorfer, 1902, of Elymnias hypermnestra hainana Moore, 1878

Elymnias hypermnestra nigrescens f. depicta Fruhstorfer, 1907, of Elymnias hypermnestra hainana Moore, 1878

Elymnias hypermnestra septentrionalis Chou & Huang, 1994, of Elymnias hypermnestra hainana Moore, 1878

Elymnias smithi Moulton, 1915, of Elymnias harterti brookei Shelford, 1904

Elymnias panthera var. labuana Staudinger, 1889, of Elymnias panthera lutescens Butler, 1867

Elymnias panthera lacrima Fruhstorfer, 1904, of Elymnias panthera lutescens Butler, 1867 Elymnias defasciata Fruhstorfer, 1911, of Elymnias panthera lutescens Butler, 1867

Elymnias panthera alfredi Fruhstorfer, 1907, of Elymnias panthera lutescens Butler, 1867

Elymnias congruens photinus Fruhstorfer, 1907, of Elymnias congruens congruens Sem-

per, 1887

Elymnias congruens phaios Fruhstorfer, 1907, of Elymnias congruens congruens Semper, 1887 Elymnias congruens rafaela Fruhstorfer, 1907, of Elymnias congruens congruens Semper, 1887 Elymnias nesaea hermia Fruhstorfer, 1907, of Elymnias nesaea nesaea (Linnaeus, 1764) Elymnias nesaea cortona Fruhstorfer, 1911, of Elymnias nesaea timandra Wallace, 1869 Elymnias nesaea coelifrons Fruhstorfer, 1907, of Elymnias nesaea hypereides Fruhstorfer, 1903 Elymnias kamara Moore, [1858], of Elymnias casiphone casiphone Geyer, [1827] Elymnias kamara lombokiana Fruhstorfer, 1911, of Elymnias casiphone praetextata Fruhstorfer, 1896

Elymnias casiphone djilantik Martin, 1909, of Elymnias casiphone exclusa de Nicéville, 1898 Elymnias malelas ivena Fruhstorfer, 1911, of Elymnias malelas malelas (Hewitson, 1863) Elymnias malelas nilamba Fruhstorfer, 1911, of Elymnias malelas malelas (Hewitson, 1863) Elymnias kochi plateni Fruhstorfer, 1907, of Elymnias beza beza (Hewitson, 1877) Dyctis bioculatus Westwood, 1850, of Elymnias agondas agondas (Boisduval, 1832) Elymnias cybele opaca Fruhstorfer, 1907, of Elymnias cybele cybele (C. & R. Felder, 1860) Elymnias cybele ternatana Fruhstorfer, 1907, of Elymnias cybele cybele (C. & R. Felder, 1860) Elymnias hicetas bonthainensis Fruhstorfer, 1899, of Elymnias hicetas hicetas Wallace, 1869 Elymnias cumaea relicina Fruhstorfer, 1907, of Elymnias phrikonis Fruhstorfer, 1899

New combinations

Elymnias hypermnestra cottonis (Hewitson, 1874) (Melanitis cottonis)
Elymnias hypermnestra beatrice Fruhstorfer, 1902 (Elymnias nigrescens beatrice)
Elymnias hypermnestra jennifferae Suzuki, 2006 (Elymnias cottonis jennifferae)
Elymnias panthera lutescens Butler, 1867 (Elymnias lutescens)
Elymnias casiphone exclusa de Nicéville, 1898 (Elymnias (Melynias) exclusa)
Elymnias agondas thryallis Kirsch, 1876 (Elymnias thryallis)
Elymnias cumaea thyone Fruhstorfer, 1904 (Elymnias thyone)

Resurrected combination

Elymnias casiphone erinyes de Nicéville, 1895

Resurrected subspecies

Elymnias cybele adumbrata Fruhstorfer, 1907

Status changes

Elymnias ceryxoides de Nicéville, 1895 stat. rev. Elymnias panthera lutescens Butler, 1867 stat. n. Elymnias cumaea thyone Fruhstorfer, 1904 stat. n.

Elymnias bornemanni Ribbe, 1889 stat. n.
Elymnias phrikonis Fruhstorfer, 1899 stat. n.
Elymnias umbratilis Joicey & Noakes, 1915 stat. n.
Elymnias resplendens Martin, 1929 stat. n.

Incertae sedis

Elymnias merula Swinhoe, 1915 Elymnias leucocyma Godart, 1819

Species not placed in any group

Elymnias singhala Moore, [1875]

Plates

Format of each legend for specimen figures (1–22):

valid species or subspecies name_ $\bigcirc \bigcirc$ dorsal/ventral_specimen repository_current name of collection locality (Country: State/Province, Locality). D = dorsal; V = Ventral; \bigcirc = male \bigcirc = female.

Format of each legend for male genitalia figures (22-26):

valid species or subspecies_specimen repository_current locality name.

See pages 4–5 for abbreviations of specimen repositories.

Each distribution map (Figs 27–78) indicates the subspecies distributions for a single species. The species name is indicated in the lower left corner, and subspecies distributions are indicated with different colors. Red dots indicate the species type locality and black dots indicate subspecies type localities. If the type locality is vague, then the dot is positioned in the center of the area specified. Type localities are not indicated on small islands, where a dot would obscure the landmass on the map.

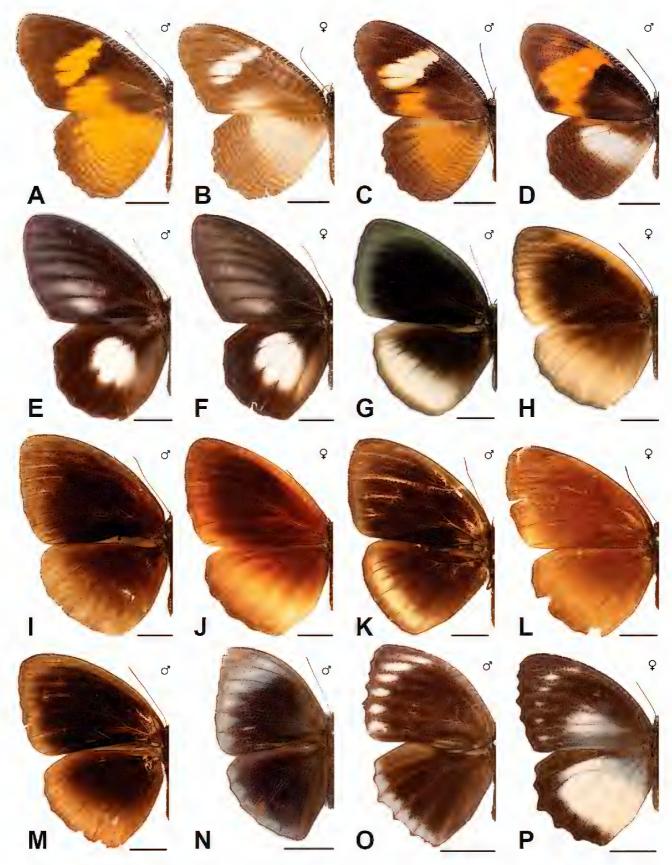


Figure I. A bammakoo bammakoo & D NHM central Africa B bammakoo bammakoo & D NHM collection locality unknown C bammakoo bammakoo & D NMNH Central African Republic: Bangui D bammakoo rattrayi & D NMNH Uganda: Bwamba E paradoxa & D NHM Indonesia: Papua, Weyland Mountains F paradoxa & D NHM Indonesia: Papua, Weyland Mountains G papua papua & D NHM Indonesia: Papua, Yos Sudarso Bay; Syntype of Elymnias papua viridescens H papua papua & D NHM Indonesia: Papua, Yos Sudarso Bay; Syntype of Elymnias papua viridescens I papua papua & D NHM Papua New Guinea J papua papua & D NHM Papua New Guinea K papua cinereomargo & D NHM Indonesia: Papua, Biak L papua cinereomargo & D NHM Indonesia: Papua, Biak L papua cinereomargo & D NHM Indonesia: Papua, Biak M papua lactentia & D NHM Indonesia: West Papua, Raja Ampat Regency, Waigeo N esaca andersonii & D KUTH Thailand: Yala, Than To O esaca maheswara & D NHM Indonesia: Java P esaca maheswara & D NHM Indonesia: Java

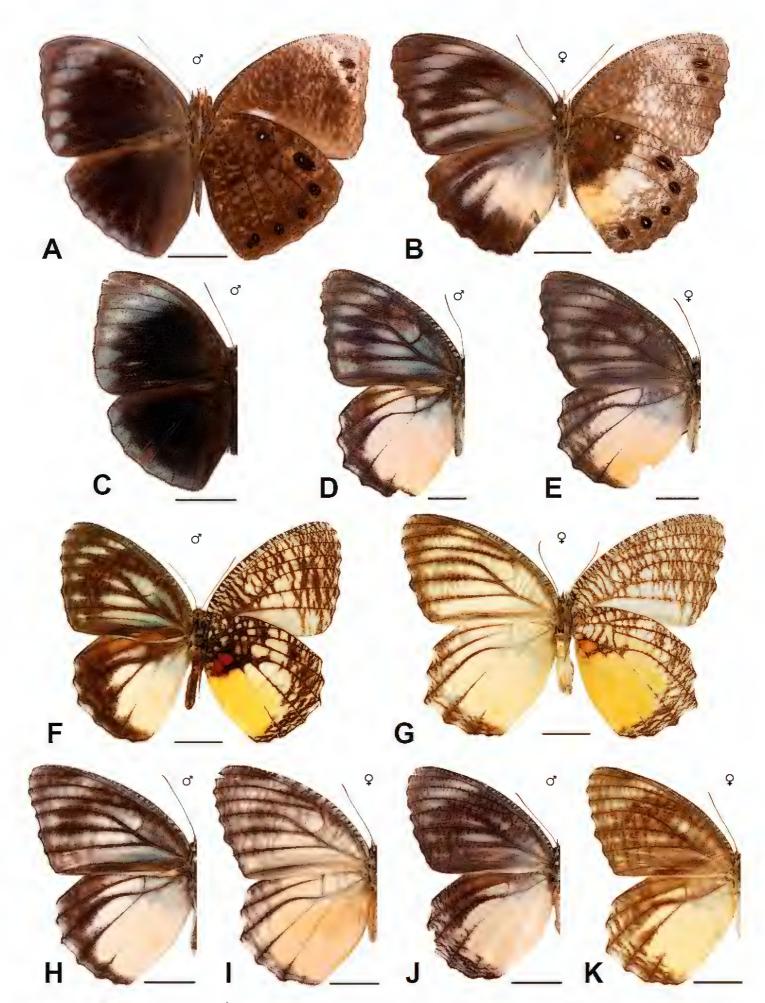


Figure 2. A esaca leontina ♂ D+V NHM Indonesia: North Sumatra, Nias **B** esaca leontina ♀ D+V NHM Indonesia: North Sumatra, Nias **C** esaca esaca ♂ D KUTH Thailand: Yala, Than To **D** vasudeva ♂ D KUTH Thailand: Kanchanburi, Sri Sawat **E** vasudeva ♀ D KUTH Thailand: Chaiyaphum, Phu Khieo **F** vasudeva ♂ D+V NHM India: Assam **G** vasudeva ♀ D+V NHM India: Assam **H** vasudeva ♂ D NHM India: Meghalaya, Khasi Hills **J** vasudeva ♂ D DNPFIC Thailand: Kanchanaburi **K** vasudeva ♀ D NHM India: Assam.

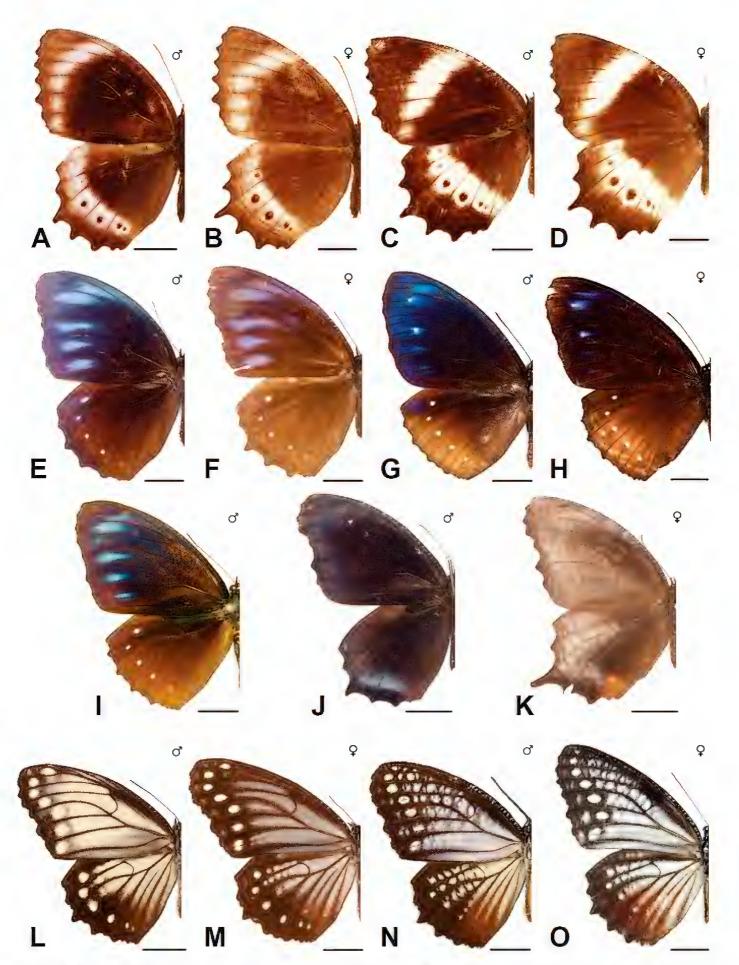


Figure 3. A dara bengena ♂ D NHM Indonesia: West Java **B** dara bengena ♀ D NHM Indonesia: West Java **C** dara daedalion ♂ D NHM Myanmar **D** dara daedalion ♀ D NHM Myanmar **E** patna patna ♂ D NHM India: Sikkim **F** patna patna ♀ D NHM India: West Bengal, Darjeeling, Pedong **G** patna "inayoshii" (nomem nudum) ♂ D KUTH Thailand: Ranong; Holotype **H** patna "inayoshii" (nomen nudum) ♀ D KUTH Thailand: Trang, Khao Chong; Paratype **I** patna hanitschi ♂ D NHM Peninsular Malaysia **J** peali ♂ D NHM India: Assam, Sivasagar **K** peali ♀ D NHM India: Assam; Holotype **L** ceryx ♂ D NHM Indonesia: West Java, Mt. Gede **M** ceryx ♀ D NHM Indonesia: West Java, Mt. Gede **N** ceryxoides ♂ D MCZ Indonesia: North Sumatra, Mt. Sinabung **O** ceryxoides ♀ D UPC Indonesia: West Sumatra.

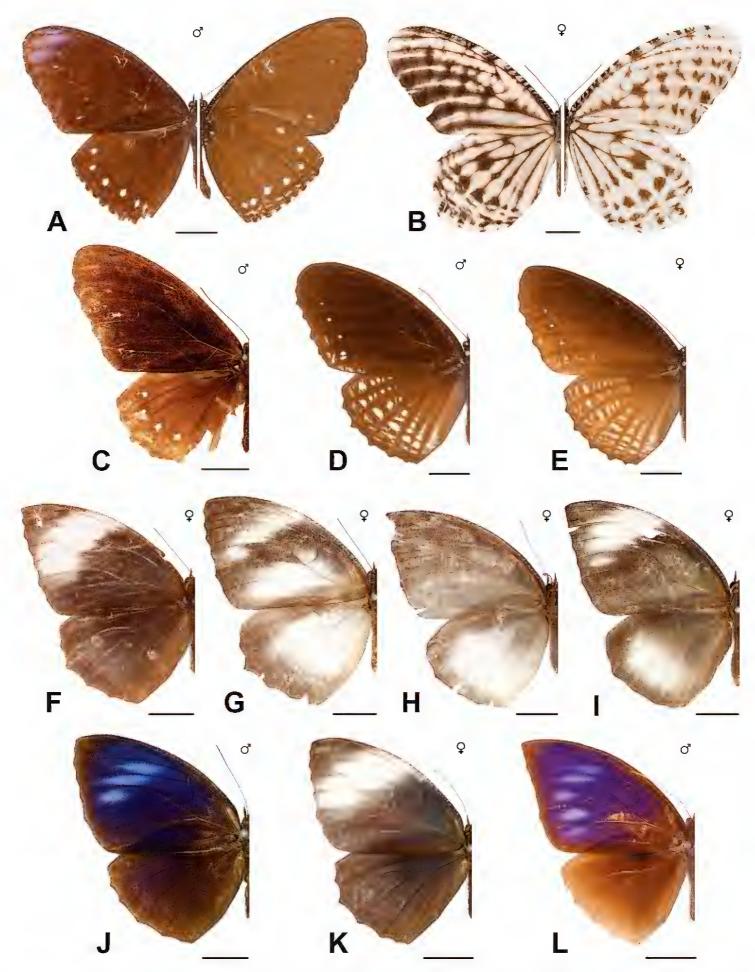


Figure 4. A kuenstleri kuenstleri \circlearrowleft D+V NHM Specimen locality unknown **B** kuenstleri kuenstleri \hookrightarrow D+V NHM Peninsular Malaysia: Selangor, Bukit Kutu **C** kuenstleri rileyi \circlearrowleft D NHM Borneo **D** pellucida \circlearrowleft D NHM Malaysia: Sabah, Mt. Kinabalu **E** pellucida \hookrightarrow D NHM Malaysia: Sabah, Mt. Kinabalu **F** penanga penanga \hookrightarrow D NHM Malaysia **G** penanga penanga \hookrightarrow D NHM Singapore; Allotype of Elymnias abrisa **H** penanga penanga \hookrightarrow D NHM Peninsular Malaysia: Penang; Holotype of Elymnias penanga penanga f. johnsoni **I** penanga sumatrana \hookrightarrow D NHM Indonesia: Sumatra; Holotype **J** penanga konga \circlearrowleft D NHM North Borneo **K** penanga konga \circlearrowleft D NHM North Borneo **L** penanga chelensis \circlearrowleft D NHM Thailand: Ranong.

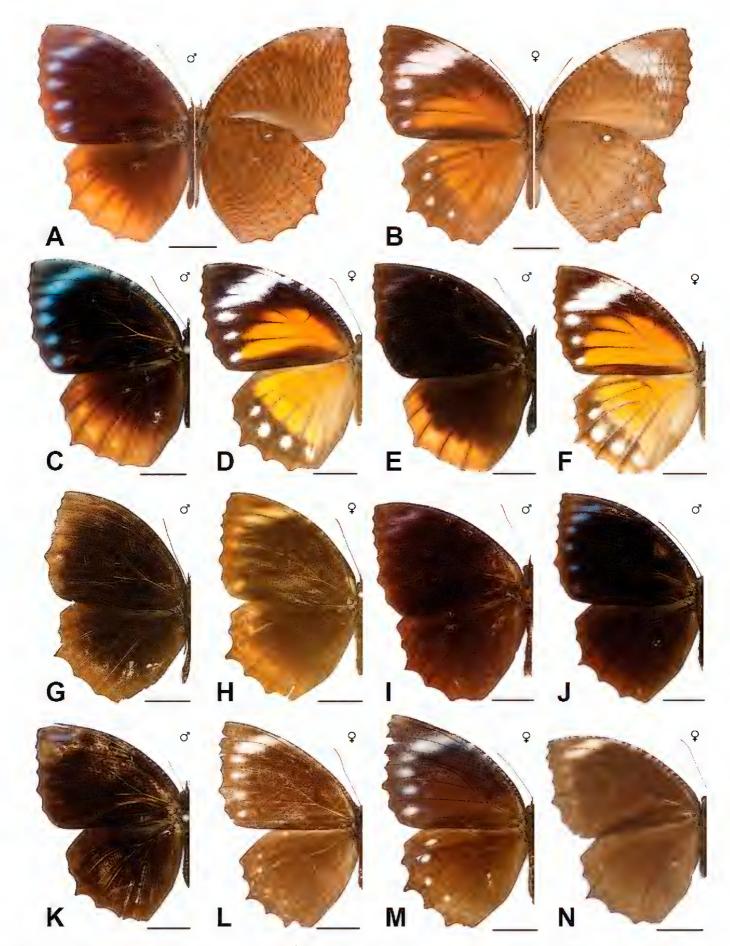


Figure 5. A hypermnestra hypermnestra ♂ D+V NHM Indonesia: Java, Bogor **B** hypermnestra hypermnestra ♀ D+V NHM Indonesia: Java, Bogor **C** hypermnestra undularis ♂ D NHM India: Assam **D** hypermnestra undularis ♀ D NHM India: Sikkim **E** hypermnestra fraterna ♂ D NHM Sri Lanka **F** hypermnestra fraterna ♀ D NHM Sri Lanka **G** hypermnestra cottonis ♂ D NHM India: Andaman Islands **H** hypermnestra cottonis ♀ D NHM India: Andaman Islands **I** hypermnestra nigrescens ♂ D NHM Brunei: Tutong **J** hypermnestra nigrescens ♂ D NHM East Malaysia: Sarawak, Mt. Marapok **K** hypermnestra nigrescens ♀ D NHM East Malaysia: Labuan; Holotype of Elymnias hecate **L** hypermnestra nigrescens ♀ D NHM East Malaysia: Sarawak, Mt. Mulu **M** hypermnestra nigrescens "f. pseudagina" ♀ D NHM East Malaysia: Sarawak **N** hypermnestra nigrescens ♀ D NHM Indonesia: Riau Islands.

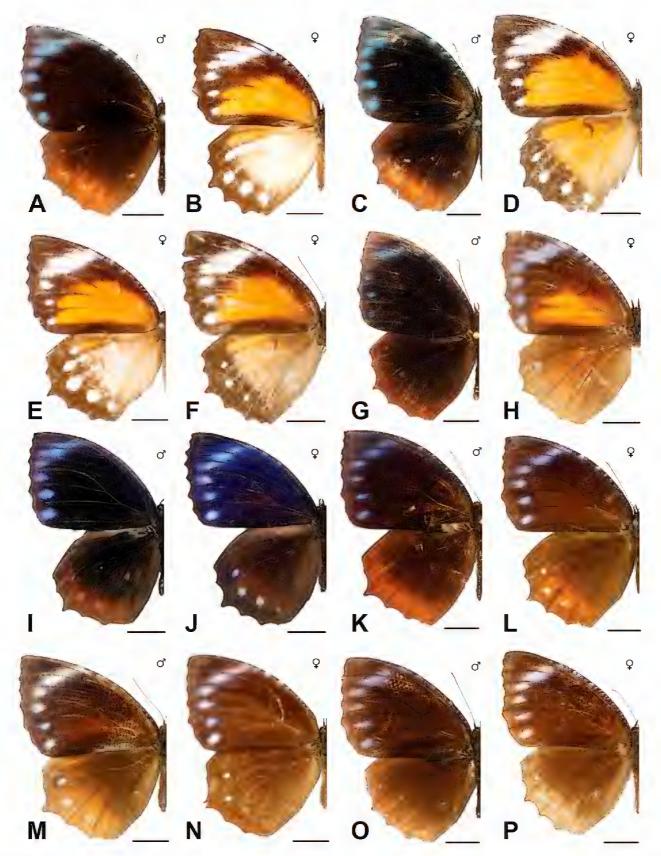


Figure 6. A hypermnestra tinctoria ♂ D NHM Myanmar: Bago B hypermnestra tinctoria ♀ D NHM Myanmar: Ayeyarwady, Pathein C hypermnestra tinctoria ♂ D NHM Thailand: Bangkok D hypermnestra tinctoria ♀ D NHM Thailand: Bangkok E hypermnestra tinctoria ♀ D NHM Myanmar: Tanintharyi; Syntype of Elymnias hypermnestra tinctoria f. paraleuca F hypermnestra tinctoria ♀ D NHM Peninsular Malaysia: Kedah, Langkawi Island G hypermnestra discrepens ♂ D NSYSU Peninsular Malaysia: Penang H hypermnestra discrepens ♀ D NHM Peninsular Malaysia: Penang; Allotype I hypermnestra hainana ♂ D NSYSU Taiwan: Kaohsiung I hypermnestra hainana ♀ D NSYSU Taiwan: Kaohsiung K hypermnestra hainana ♂ D NHM Vietnam L hypermnestra hainana ♀ D NHM Vietnam M hypermnestra hainana (f. depicta) ♂ D NHM Vietnam: Haiphong N hypermnestra hainana (f. depicta) ♀ D NHM Vietnam: Haiphong O hypermnestra orientalis ♂ D NHM Indonesia: East Nusa Tenggara, Flores, Ende Island; Holotype of Elymnias nigrescens dohertyi P hypermnestra orientalis ♀ D NHM Indonesia: East Nusa Tenggara, Flores.

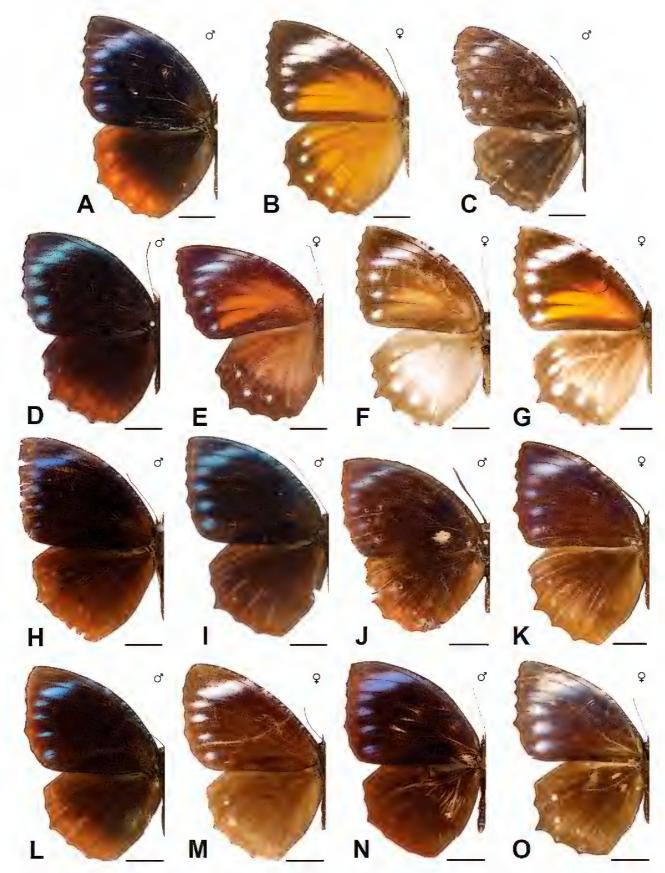


Figure 7. A hypermnestra baliensis ♂ D NHM Indonesia: Bali B hypernmestra baliensis ♀ D NHM Indonesia: Bali C hypermnestra baliensis ♂ D NHM Indonesia: Bali; Holotype of Elymnias nigrescens bulelenga D hypermnestra tinctoria ♂ D KUTH Thailand: Chiang Mai E hypermnestra tinctoria ♀ D KUTH Thailand: Chanthaburi F hypermnestra violetta ♀ D NHM Thailand: Sri Racha; Holotype of Elymnias hypermnestra violetta f. obfuscata G hypermnestra meridonalis ♀ D NHM southern Vietnam; Holoype of Elymnias meridionalis f. orphnia H hypermnestra beatrice ♂ D NHM Peninsular Malaysia: Perak, Taiping I hypermnestra beatrice ♂ D NHM Peninsular Malaysia: Pahang, Gunung Tahan J hypermnestra beatrice ♂ D MCZ Peninsular Malaysia: Perak K hypermnestra beatrice ♀ D MCZ Singapore L hypermnestra sumbana ♂ D NHM Indonesia: East Nusa Tenggara, Sumba M hypermnestra sumbana ♀ D NHM Indonesia: East Nusa Tenggara, Sumba N hypermnestra decolorata ♂ D NHM Indonesia: Sumatra O hypermnestra decolorata ♀ D NHM Indonesia: Sumatra.

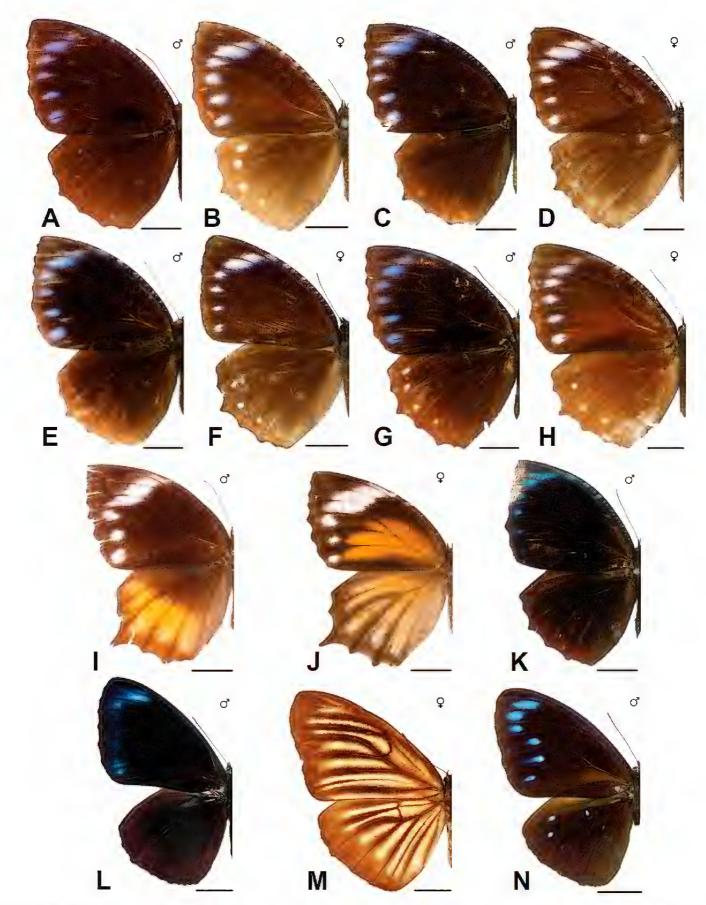


Figure 8. A hypermnestra sumbawana ♂ D NHM Indonesia: West Nusa Tenggara, Sumbawa **B** hypermnestra sumbawana ♀ D NHM Indonesia: West Nusa Tenggara, Sumbawa **C** hypermnestra timorensis ♂ D NHM East Timor: Dili **D** hypermnestra timorensis ♀ D NHM East Timor: Dili **E** hypermnestra alorensis ♂ D NHM Indonesia: East Nusa Tenggara, Adonara **F** hypermnestra alorensis ♀ D NHM Indonesia: East Nusa Tenggara, Adonara **G** hypermnestra uemurai ♂ D NHM Indonesia: West Nusa Tenggara, Lombok **H** hypermnestra uemurai ♀ D NHM Indonesia: West Nusa Tenggara, Lombok **I** caudata ♂ D NHM Myanmar (specimen is likely mislabeled) **J** caudata ♀ D NHM India: Kerala, Malabar **K** merula ♂ D NHM Sri Lanka: Central Province, Kandy; Holotype **L** nepheronides nepheronides ♂ D HSPC Indonesia: East Nusa Tenggara, Flores **M** nepheronides nepheronides ♀ D NHM Indonesia: East Nusa Tenggara, Flores **N** nepheronides tamborana ♂ D OPC Indonesia: Sumbawa, Mt. Sengenges; Holotype.

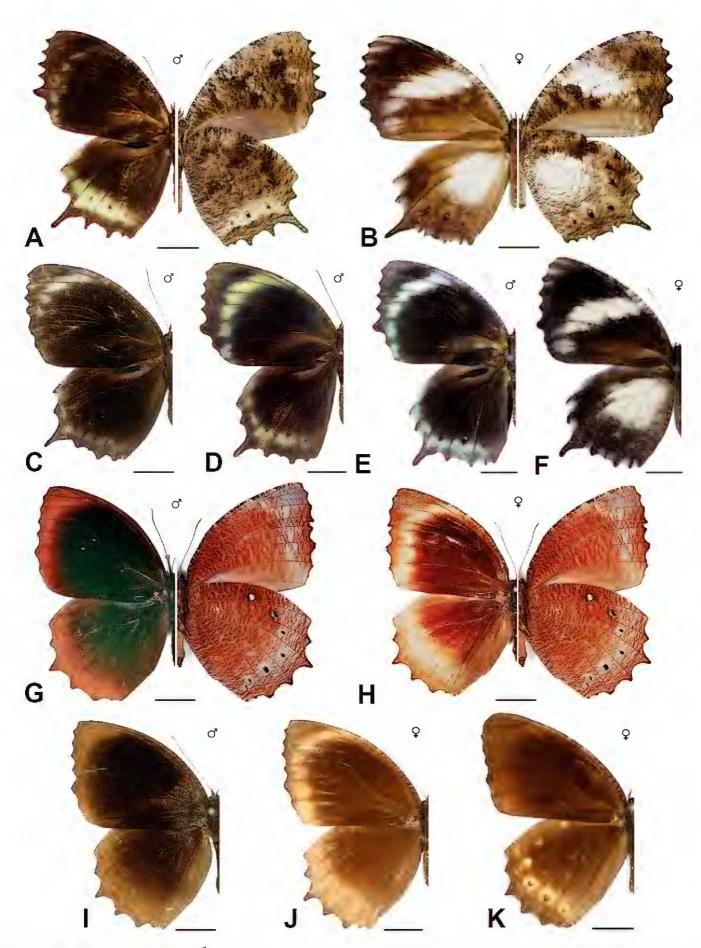


Figure 9. A harterti harterti ♂ D+V OPC Malaysia: Perak, Batang Padang, Tapah **B** harterti harterti ♀ D+V OPC Malaysia: Perak, Batang Padang, Tapah **C** harterti brookei ♂ D NHM collection locality unknown **D** harterti lautensis ♂ D OPC Indonesia: South Kalimantan, Laut Island; Holotype **E** harterti arbaimuni ♂ D OPC Indonesia: central Sumatra, Jambi; Holotype **F** harterti arbaimuni ♀ D OPC Indonesia: central Sumatra, Jambi **G** parce justini ♂ D+V SMFD Philippines: Palawan Province, Calamian Islands, Busuanga Island, Coron; Holotype **H** parce justini ♀ D+V SMFD Philippines: Palawan Province, Calamian Islands, Busuanga Island, Coron; Paratype **I** parce parce ♂ D NHM Philippines: Palawan **J** parce parce ♀ D NHM Philippines: Palawan **K** panthera enganica ♀ D NHM Indonesia: Bengkulu, Enggano Island.

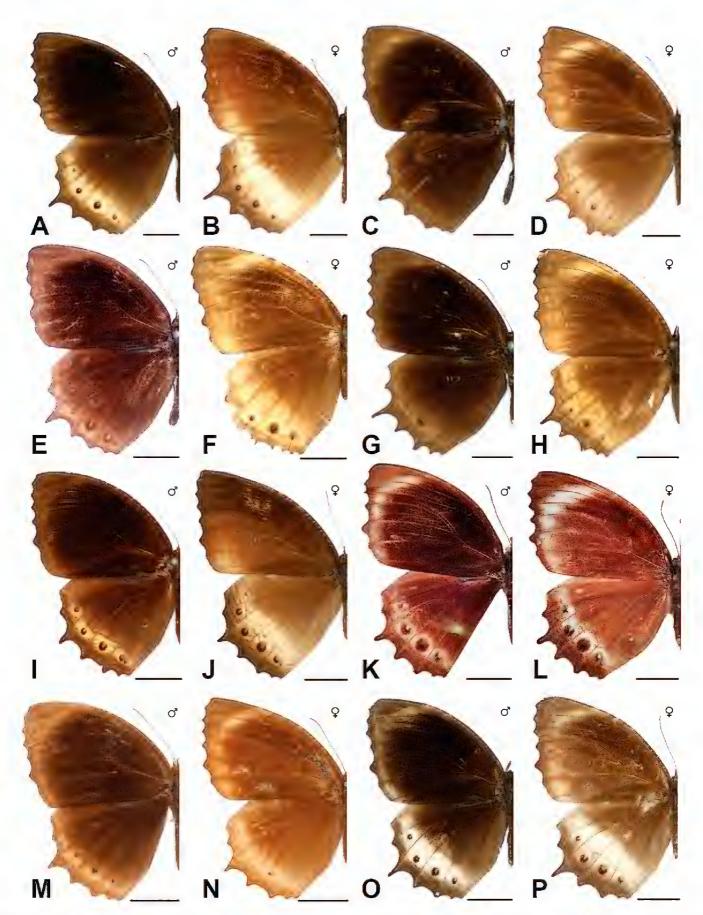


Figure 10. A panthera panthera & D NHM Peninsular Malaysia **B** panthera panthera & D NHM Peninsular Malaysia **C** panthera dusara & D NHM Indonesia: Java **D** panthera dusara & D NHM Indonesia: Java **E** panthera mimus & D NHM Indonesia: Nicobar Islands **F** panthera mimus & D NHM India: Nicobar Islands **G** panthera dolorosa & D NHM Indonesia: North Sumatra, Nias **H** panthera dolorosa D NHM Indonesia: North Sumatra, Nias **I** panthera lutescens & D NHM North Borneo **J** panthera lutescens & D NHM East Malaysia: Sarawak **K** panthera suluana & D SMFD collection locality unknown **L** panthera suluana & D SMFD Philippines: Tawi-tawi, Mapun Island **M** panthera tautra & D NHM Indonesia: Sumatra, Bengkalis, Senggoro **N** panthera tautra & D NHM Indonesia: Sumatra, Bengkalis, Senggoro **O** panthera arikata & D NHM Indonesia: Riau Islands, Natuna **P** panthera arikata & D NHM Indonesia: Riau Islands, Natuna.

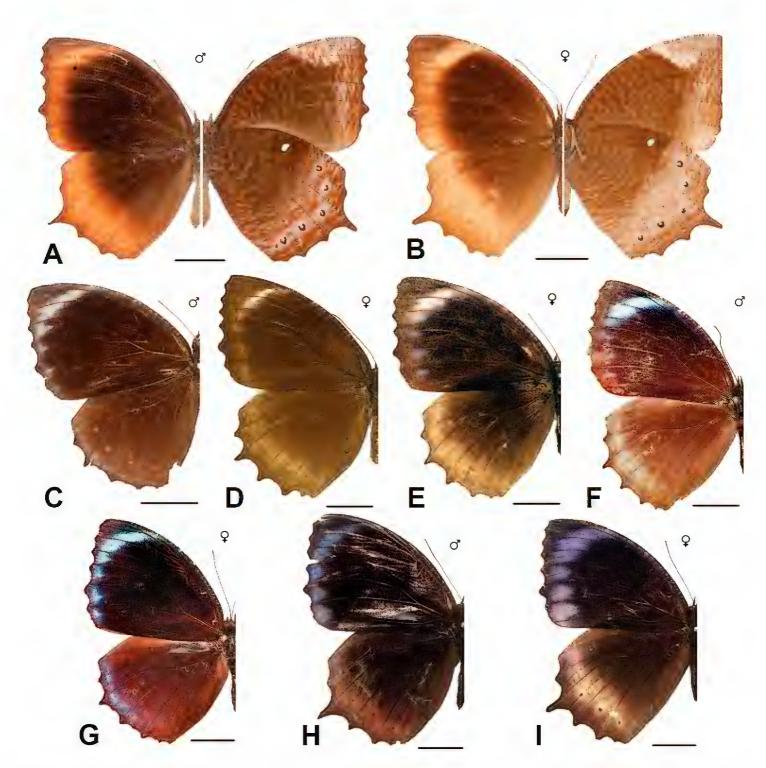


Figure II. A obnubila ♂ D+V NHM MALAYSIA: Perak **B** obnubila ♀ D+V NHM THAILAND: Ranong **C** congruens congruens ♂ D NHM PHILIPPINES: Cebu, Camotes Island **D** congruens subcongruens ♀ D NHM PHILIPPINES: Mindoro **E** congruens endida ♂ D SMFD PHILIPPINES: Bohol **F** congruens endida ♀ D SMFD PHILIPPINES: Bohol **G** congruens congruens ♀ D NMNH PHILIPPINES: Mindanao, Davao **H** miyagawai ♂ D SPC VIETNAM: Lam Dong, Loc Bao; Paratype.

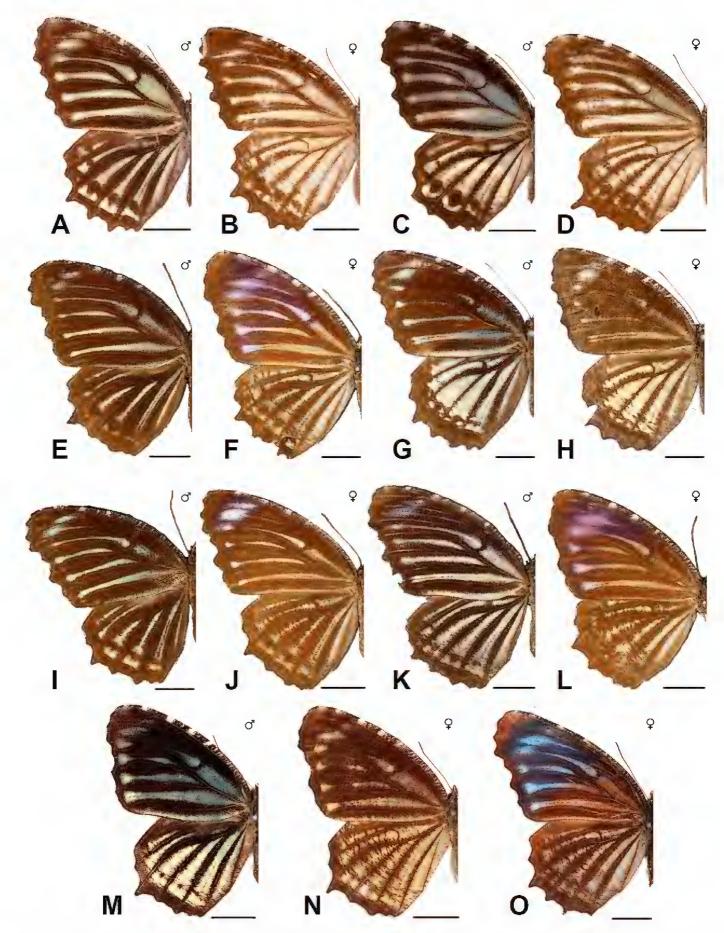


Figure 12. A nesaea nesaea ♂ D NHM Indonesia: Java B nesaea nesaea ♀ D NHM Indonesia: Java C nesaea timandra ♂ D NHM India: Meghalaya, Khasi Hills D nesaea timandra ♀ D NHM India: Meghalaya, Khasi Hills E nesaea laisidis ♂ D MCZ Indonesia: Sumatra F nesaea laisidis ♀ D MCZ Indonesia: West Sumatra, Padang G nesaea baweana ♂ D NHM Indonesia: East Java, Gresik Regency, Bawean H nesaea baewana ♀ D NHM Indonesia: East Java, Gresik Regency, Bawean I nesaea neolais ♂ D MCZ Indonesia: North Sumatra, Nias, Dymna J nesaea neolais ♀ D MCZ Indonesia: North Sumatra, Nias K nesaea hypereides ♂ D MCZ East Malaysia: Sabah, Sandakan L nesaea hypereides ♀ D MCZ East Malaysia: Sabah, Sandakan M nesaea apelles ♂ D KUTH Thailand: Samut Sakhon N nesaea apelles ♀ D KUTH Thailand: Satun, Thale Ban.

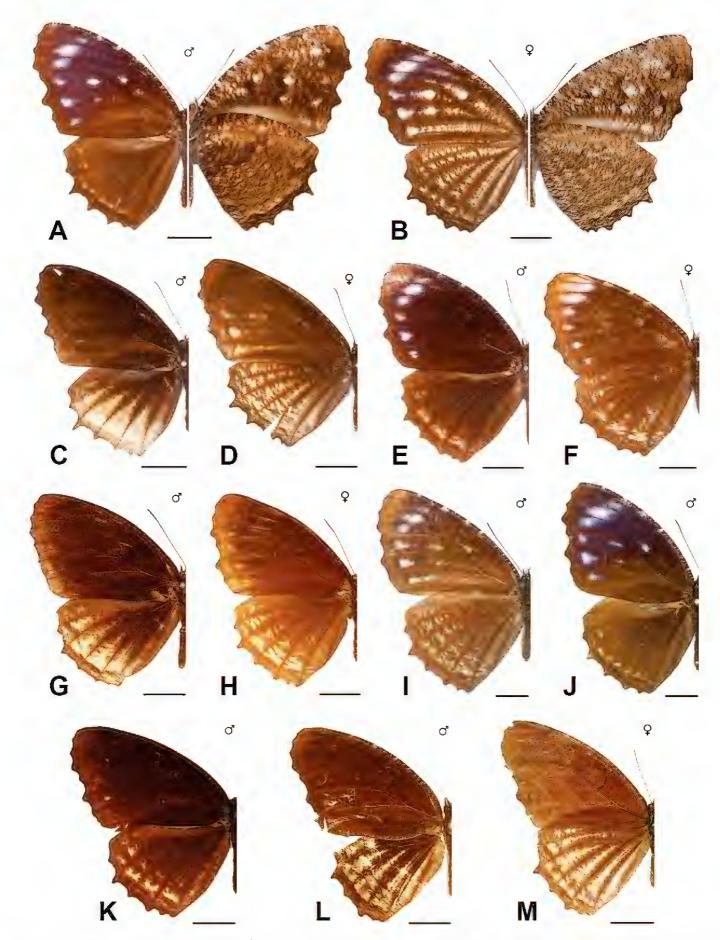


Figure 13. A casiphone casiphone ♂ D+V NHM Indonesia: Java B casiphone casiphone ♀ D+V NHM Indonesia: Java C casiphone kamara ♂ D NHM Indonesia: Java D casiphone kamara ♀ D NHM Indonesia: Java E casiphone praetextata ♂ D NHM Indonesia: West Nusa Tenggara, Lombok F casiphone praetextata ♀ D NHM Indonesia: West Nusa Tenggara, Lombok G casiphone praetextata (=kamara lombokiana) ♂ D NHM Indonesia: West Nusa Tenggara, Lombok H casiphone praetextata (=kamara lombokiana) ♀ D NHM Indonesia: West Nusa Tenggara, Lombok I casiphone praetextata (=kamara lombokiana) ♀ D NHM Indonesia: West Nusa Tenggara, Lombok; Syntype of Elymnias kamara lombokiana J casiphone alumna ♂ D NHM Indonesia: East Java, Blitar K casiphone exclusa ♂ D NHM Indonesia: Bali L casiphone erinyes ♂ D NHM Indonesia: Sumatra

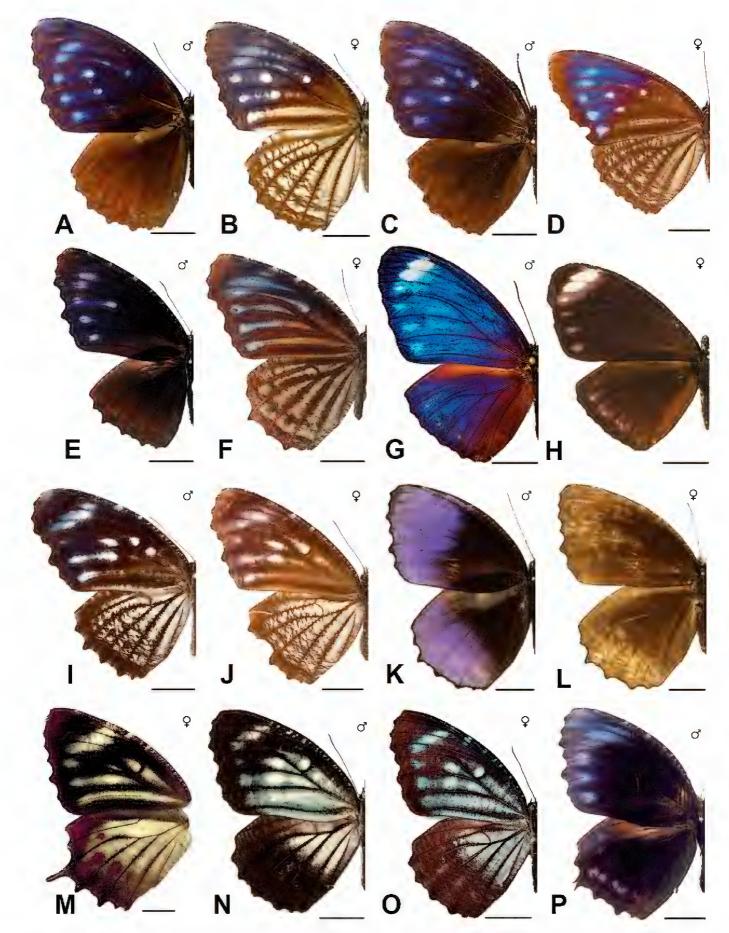


Figure 14. A malelas \lozenge D NHM India: Sikkim **B** malelas \lozenge D NHM India: Sikkim **C** malelas \lozenge D MCZ Vietnam **D** malelas \lozenge D KUTH Thailand: Chiang Mai **E** saueri \lozenge D IPC Thailand: Phetchabun **F** saueri \lozenge D NMNH Malaysia: Johor, Mersing to Kluang **G** kochi \lozenge D SMFD Philippines: Luzon, Sierre Madre Mountain Range **H** kochi \lozenge D PNM Philippines: Luzon, Sierre Madre Mountain Range **I** casiphonides casiphonides \lozenge D NHM Philippines: Mindanao **J** casiphonides casiphonides \lozenge D NHM Philippines: Mindanao **K** nelsoni \lozenge D UPC Indonesia: West Sumatra, Mentawai Regency, Sipora **L** nelsoni \lozenge D UPC Indonesia: West Sumatra, Mentawai Regency, Sipora **M** amoena \lozenge D MCZ Indonesia: Sumba, Kombapari Forest **N** kanekoi \lozenge D NHM Philippines: Negros **O** kanekoi \lozenge D SMFD Philippines: Negros **P** saola \lozenge D NHM Vietnam; Holotype.

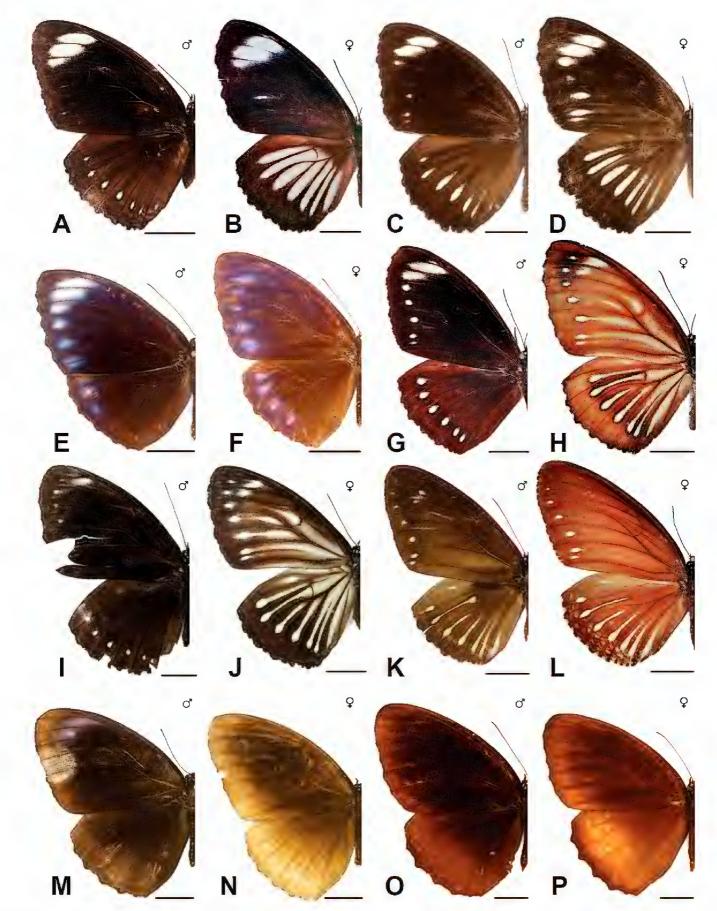


Figure 15. A melias melias & D NMNH Philippines: Luzon, Cavite, Puerto Azul B melias melias & D SMFD Philippines: Luzon, Sierre Madre Mountains C melias malis & D NHM Philippines: Quezon, Polillo Island D melias malis & D NHM Philippines: Luzon, Los Baños E beza beza & D NHM Philippines: Mindanao F beza beza & D NHM Philippines: Mindanao G sansoni sansoni & D SMFD Philippines: Negros H sansoni sansoni & D SMFD Philippines: Negros I sansoni aklanensis & D UPC Philippines: Panay, Aklan; Paratype J sansoni aklanensis & D UPC Philippines: Panay, Aklan; Paratype K luteofasciata & D OPC Philippines: Mindanao, Penangudltan, Upian River, City of Davao; Holotype L luteofasciata & D SMFD Philippines: Mindanao, South Cotabato, Mt. Matutum M vitellia vitellia & D NHM Indonesia: Maluku, Ambon N vitellia vitellia & D NHM Indonesia: Maluku, Ambon O vitellia viminalis & D NHM Indonesia: Maluku, Buru P vitellia viminalis & D NHM Indonesia: Maluku, Buru.

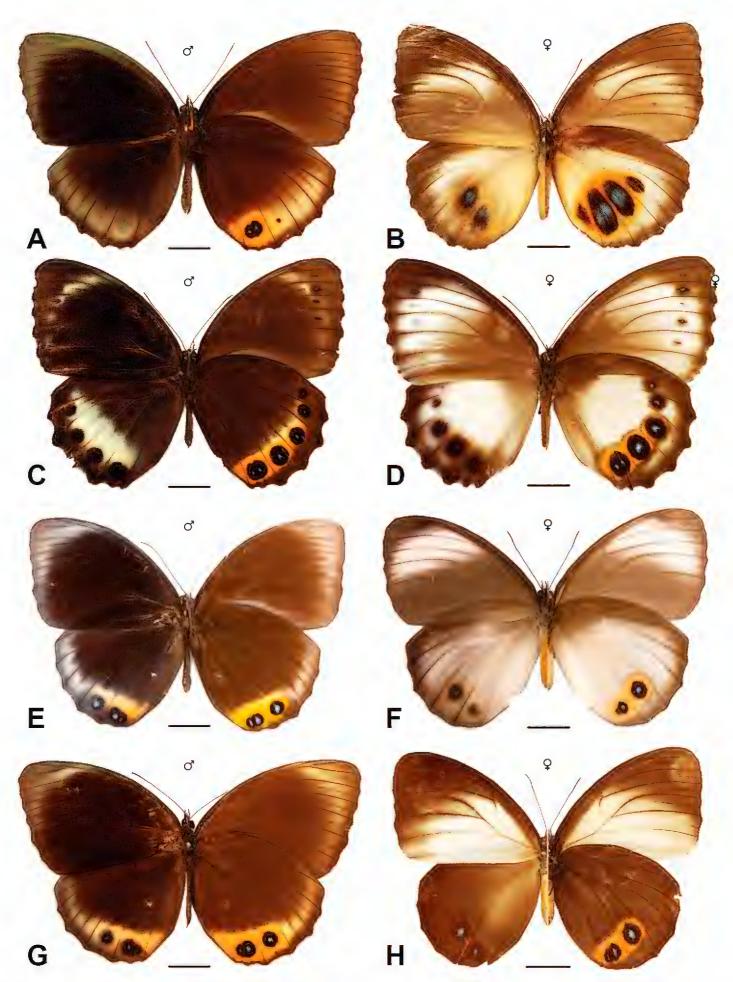


Figure 16. A agondas agondas ♂ D+V NHM Indonesia: West Papua **B** agondas agondas ♀ D+V NHM Indonesia: West Papua **C** agondas melane ♂ D+V NHM Indonesia: Maluku, Kei Island **D** agondas melane ♀ D+V NHM Indonesia: Maluku, Kei Island **E** agondas glaucopis ♂ D+V NHM Papua New Guinea: Oro Province, Kumusi River **F** agondas glaucopis ♀ D+V NHM Papua New Guinea: Oro Province, Kumusi River **G** agondas melanippe ♂ D+V NHM Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg **H** agondas melanippe ♀ D+V NHM Papua New Guinea: Morobe Province, Huon Peninsula, Sattelberg.

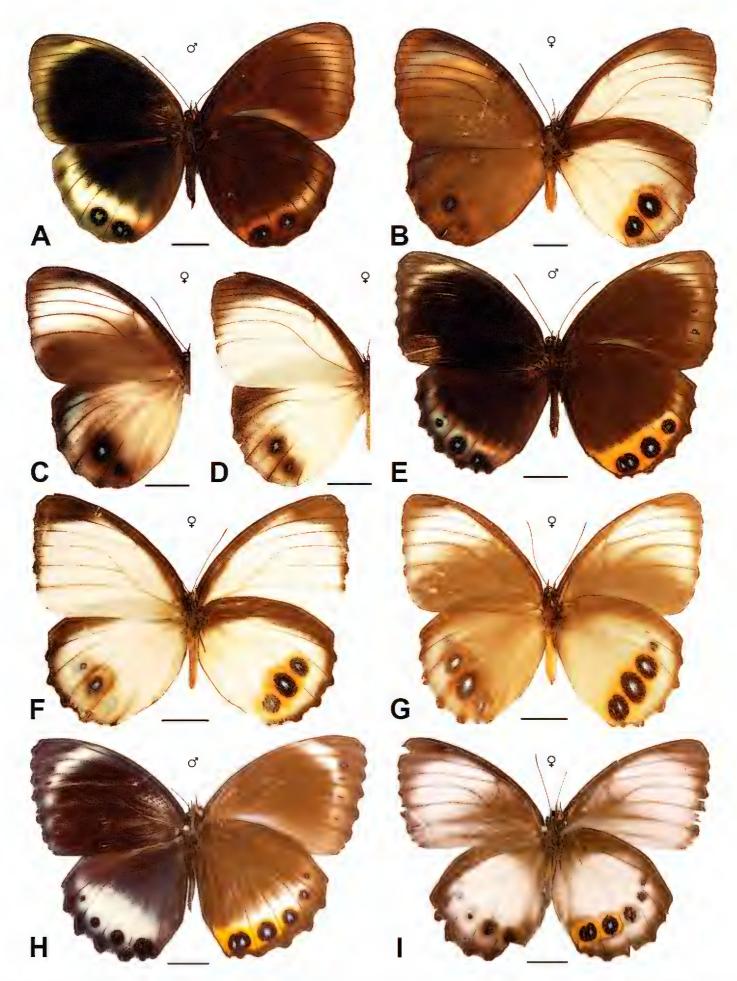


Figure 17. A agondas melanthes ♂ D+V NHM Papua New Guinea: Milne Bay, Woodlark Island **B** agondas melanthes ♀ D+V NHM Papua New Guinea: Milne Bay, Woodlark Island **C** agondas melanthes ♀ D NHM Papua New Guinea: Milne Bay, Woodlark Island **D** agondas melanthes ♀ D NHM Papua New Guinea: Milne Bay, Woodlark Island **E** agondas aruana ♂ D+V NHM Indonesia: Maluku, Aru **F** agondas aruana ♀ D+V NHM Indonesia: Maluku, Aru **H** agondas ssp. ♂ D+V NHM Indonesia: Maluku, Tanimbar I agondas ssp. ♀ D+V NHM Indonesia: Maluku, Tanimbar I agondas ssp. ♀ D+V NHM Indonesia: Maluku, Tanimbar.

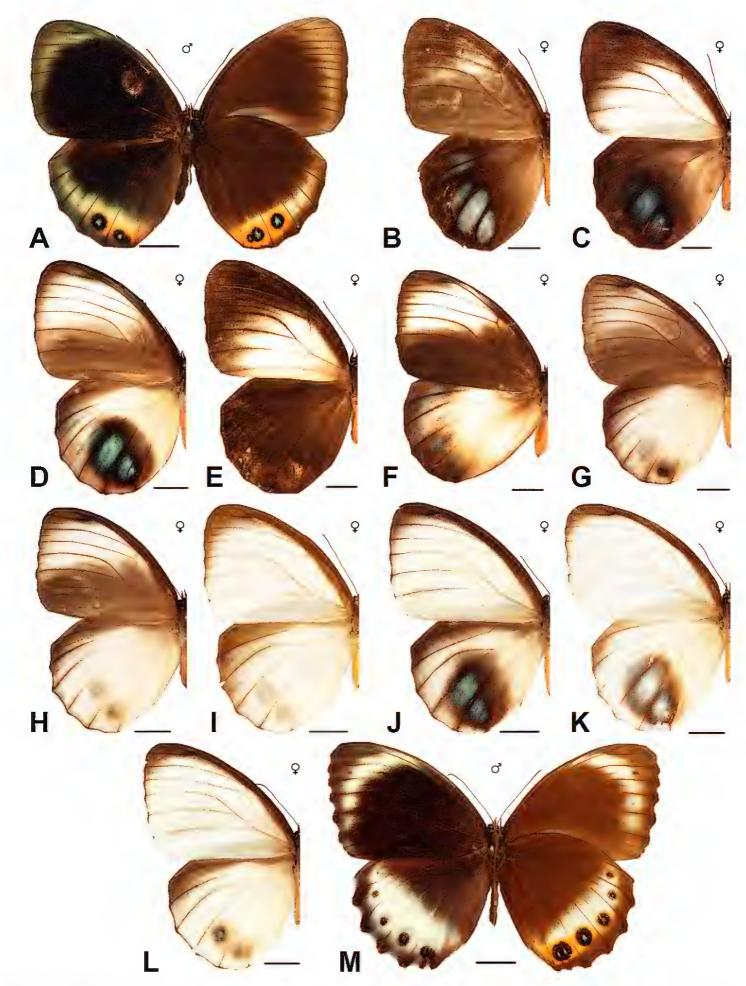


Figure 18. A agondas melagondas ♂ D+V NHM New Guinea **B** agondas melagondas ♀ D NHM New Guinea **C** agondas melagondas ♀ D NHM New Guinea **D** agondas melagondas ♀ D NHM New Guinea **E** agondas melagondas ♀ D NHM New Guinea **F** agondas melagondas ♀ D NHM New Guinea **G** agondas melagondas ♀ D NHM New Guinea **H** agondas melagondas ♀ D NHM New Guinea **I** agondas melagondas ♀ D NHM New Guinea **K** agondas melagondas ♀ D NHM New Guinea **M** agondas goramensis ♂ D+V NHM Indonesia: Maluku, East Seram Regency, Gorong Island.

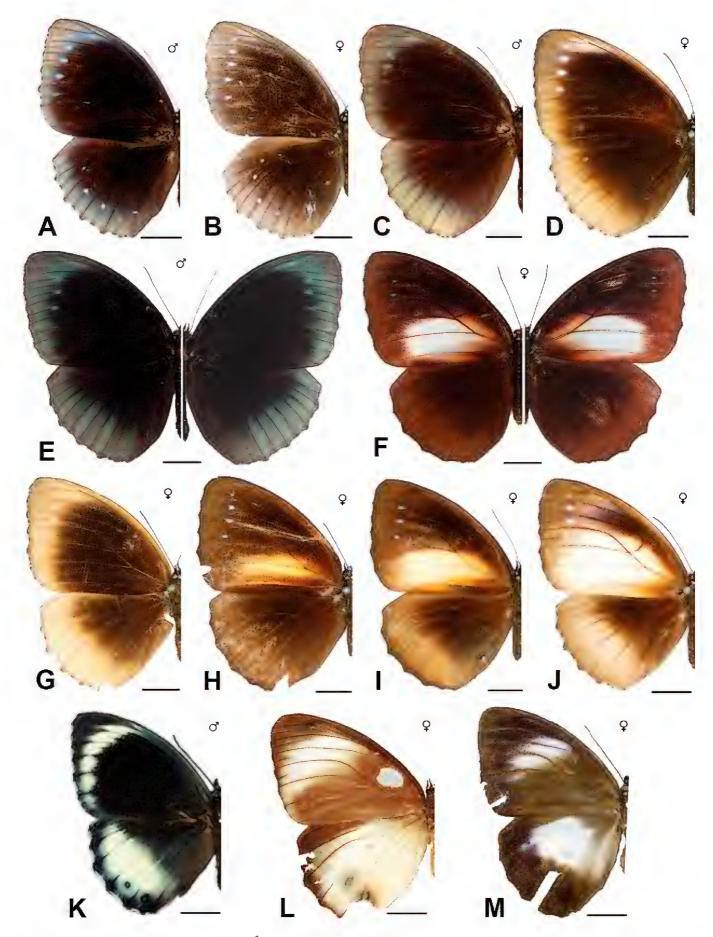


Figure 19. A agondas dampierensis ♂ D NHM Papua New Guinea: Madang, Karkar Island; Syntype B agondas dampierensis ♀ D NHM Papua New Guinea: Madang, Karkar Island C agondas thryallis ♂ D NHM Papua New Guinea D agondas thryallis ♀ D NHM Papua New Guinea E agondas thryallis ♂ D+V NMNH Papua New Guinea: East Sepik, Maprik F agondas thryallis ♀ D+V NMNH Papua New Guinea: Regia, Mapuk G agondas thryallis ♀ D NHM Indonesia: Papua, Yos Sudarso Bay H agondas thryallis ♀ D NHM Indonesia: Papua, Yos Sudarso Bay J agondas thryallis ♀ D NHM Indonesia: Papua, Yos Sudarso Bay J agondas thryallis ♀ D NHM Indonesia: Papua, Yos Sudarso Bay K agondas australiana ♂ D MCZ Australia: Queensland, Claudie River L agondas australiana ♀ D NHM Australia: Queensland M agondas australiana ♀ D MCZ Australia: Queensland, West Claudie River.

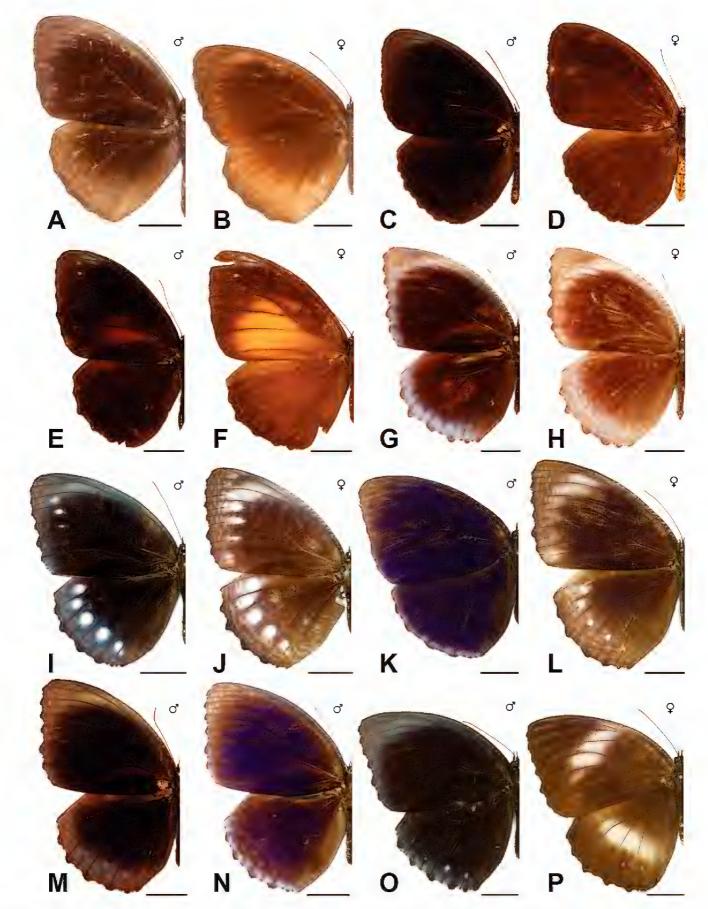


Figure 20. A cybele cybele & D NHM Indonesia: North Maluku, Halmahera **B** cybele cybele & D NHM Indonesia: North Maluku, Halmahera **C** cybele cybele & D NHM Indonesia: North Maluku, Bacan **D** cybele cybele & D NHM Indonesia: North Maluku, Bacan **E** cybele obiana & D NHM Indonesia: North Maluku, Obi **F** cybele obiana & D NHM Indonesia: North Maluku, Obi **G** cumaea cumaea & D NHM Indonesia: North Sulawesi, Menado **H** cumaea cumaea & D NHM Indonesia: North Sulawesi, Minahasa **I** hewitsoni hewitsoni & D NHM Indonesia: South Sulawesi **J** hewitsoni hewitsoni & D NHM Indonesia: Sulawesi **L** mimalon mimalon & D NHM Indonesia: Sulawesi **L** mimalon mimalon & D NHM Indonesia: South Sulawesi

N mimalon ino & D NHM Indonesia: Central Sulawesi; Holotype **O** hicetas hicetas & D NHM Indonesia: Sulawesi

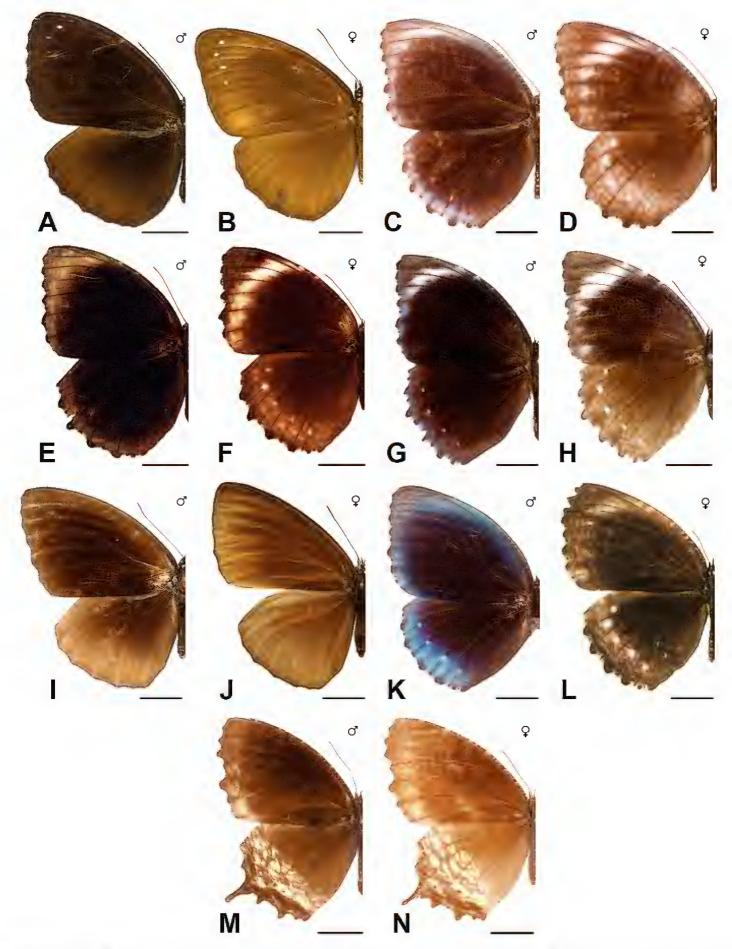


Figure 21. A holofernes ♂ D NHM Papua New Guinea: New Britain **B** holofernes ♀ D NHM Papua New Guinea: New Britain **C** bornemanni ♂ D NHM Indonesia: Central Sulawesi, Banggai **D** bornemanni ♀ D NHM Indonesia: Central Sulawesi, Banggai **E** phrikonis ♂ D NHM Indonesia: Sula Archipelago **F** phrikonis ♀ D NHM Indonesia: Sula Archipelago **G** sangira ♂ D NHM Indonesia: North Sulawesi, Talaud **I** umbratilis ♂ D NHM Indonesia: North Sulawesi, Talaud **I** umbratilis ♂ D NHM Indonesia: Papua, Biak; Holotype **J** umbratilis ♀ D OPC Indonesia: Papua, Biak **K** resplendens ♂ MCZ Indonesia: Central Sulawesi, Palu **L** resplendens ♀ MCZ Indonesia: Central Sulawesi, Palu **M** singhala ♂ D NHM Sri Lanka **N** singhala ♀ D NHM Sri Lanka.

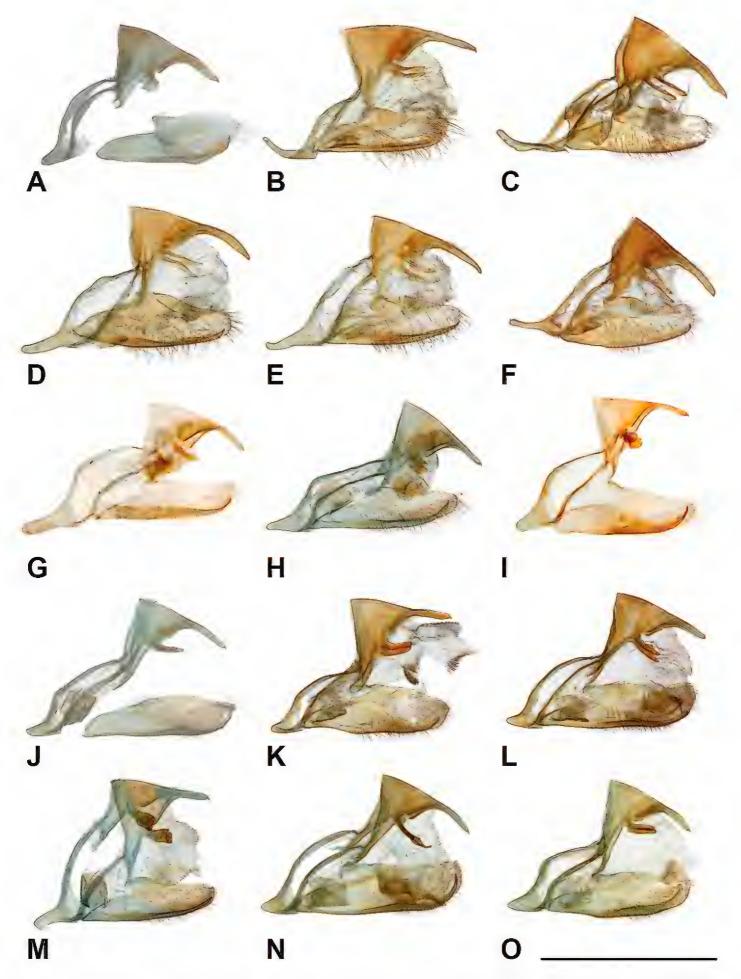


Figure 22. A bammakoo bammakoo NHM Central Africa B paradoxa NHM Indonesia: Papua, Weyland Mountains C papua cinereomargo NHM Indonesia: Papua, Biak D esaca maheswara NHM Indonesia: Java E esaca leontina NHM Indonesia: North Sumatra, Nias F vasudeva NHM India: Meghalaya, Khasi Hills G dara albofasciata MCZ Philippines: Palawan H dara bengena NHM Indonesia: Java I dara darina MCZ Peninsular Malaysia: Pahang, Cameron Highlands J patna patna NHM India: Sikkim K peali NHM India: Assam L ceryx NHM Indonesia: Java M kuenstleri NHM collection locality unknown N pellucida NHM East Malaysia: Sabah, Mt. Kinabalu O penanga chelensis NHM Thailand: Ranong.

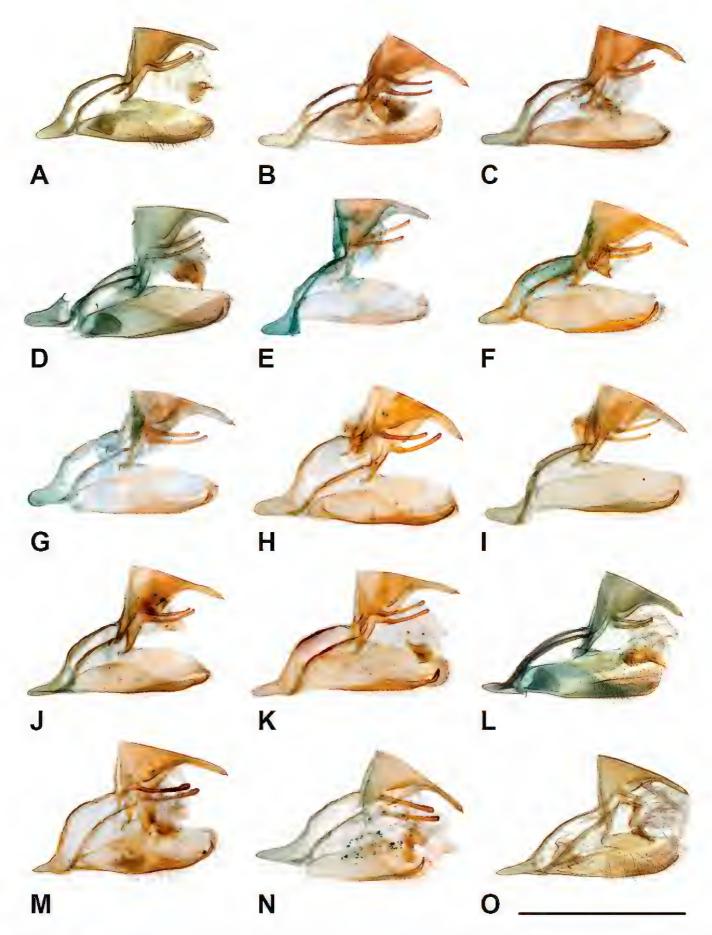


Figure 23. A hypermnestra hypermnestra NHM Indonesia: West Java, Bogor B hypermnestra hypermnestra MCZ Indonesia: Maluku, Seram C hypermnestra fraterna MCZ Sri Lanka: Western Province D hypermnestra cottonis NHM India: Andaman Islands E hypermnestra tinctoria NSYSU Thailand: Trang, Khao Chong F hypermnestra hainana NSYSU Taiwan: Kaohsiung G hypermnestra discrepans NSYSU Peninsular Malaysia: Penang H hypermnestra orientalis MCZ Indonesia: East Nusa Tenggara, Flores I hypermnestra baliensis NSYSU Indonesia: Bali J hypermnestra sumbana MCZ Indonesia: East Nusa Tenggara, Sumba K hypermnestra timorensis MCZ Indonesia: East Nusa Tenggara, Timor L caudata NHM Myanmar (specimen is likely mislabeled) M nepheronides nepheronides MCZ Indonesia: East Nusa Tenggara, Flores N parce MCZ Philippines: Palawan O panthera tautra NHM Indonesia: Sumatra, Bengkalis, Senggoro.

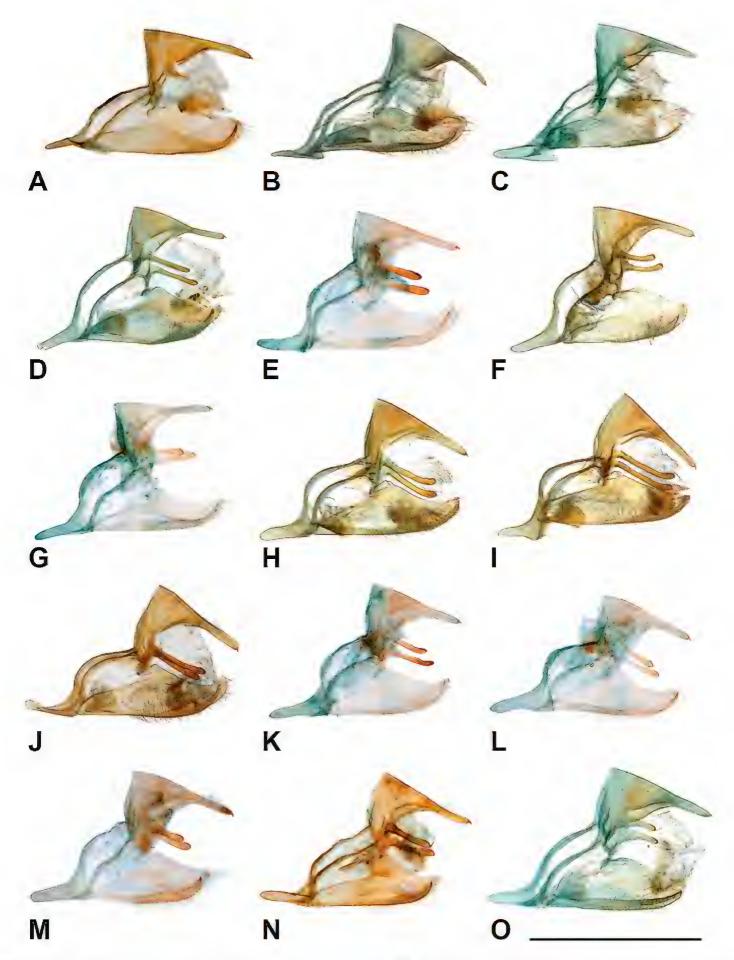


Figure 24. A panthera balina MCZ Indonesia: Bali B obnubila NHM Peninsular Malaysia: Perak C congruens congruens NHM Philippines: Cebu, Camotes Island D nesaea nesaea NHM Indonesia: Java E nesaea nesaea NSYSU Indonesia: Bali F nesaea timandra NHM India: Meghalaya, Khasi Hills G nesaea vordemani NSYSU Indonesia: East Java, Kangean Islands H casiphone casiphone NHM Indonesia: Java I casiphone casiphone NHM Indonesia: Java J casiphone praetextata NHM Indonesia: East Nusa Tenggara, Lombok K casiphone exclusa NSYSU Indonesia: Bali L casiphone alumna NSYSU Indonesia: Java M malelas NSYSU Thailand: Chiang Mai N kochi MCZ Philippines: Luzon, Sierra Madre Range, Isabela O casiphonides casiphonides NHM Philippines: Mindanao

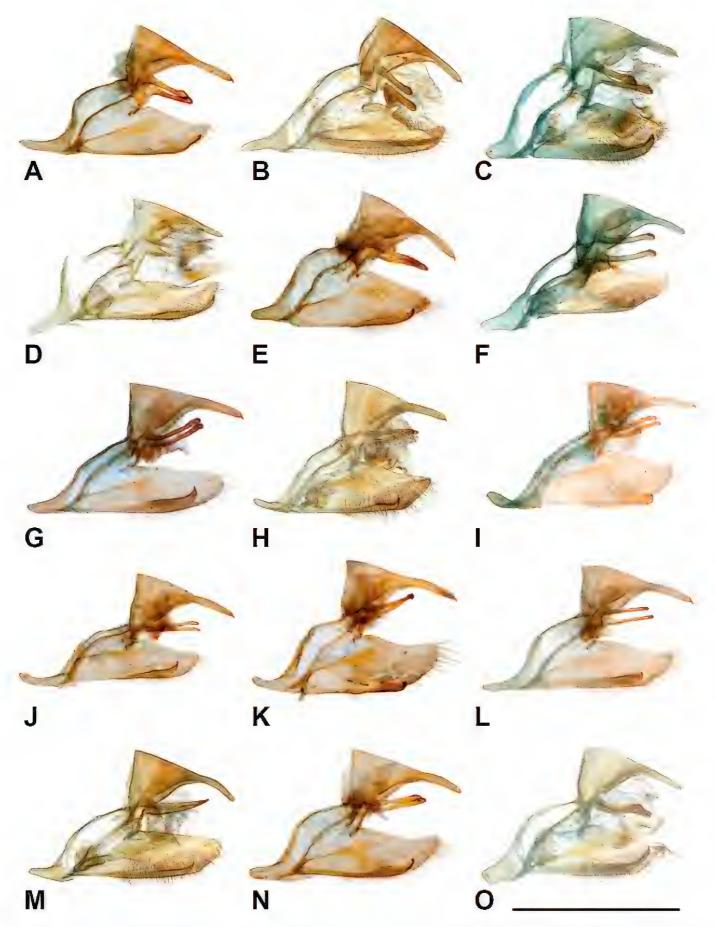


Figure 25. A nelsoni MCZ Indonesia: West Sumatra, Pagai Island **B** kanekoi NHM Philippines: Negros **C** melias malis NHM Philippines: Quezon, Polillo Island **D** beza beza NHM Philippines: Mindanao **E** sansoni aklanensis MCZ Philippines: Panay, Aklan, Mt. Madiaas **F** vitellia vitellia NHM Indonesia: Maluku, Ambon **G** vitellia viminalis MCZ Indonesia: Maluku, Buru **H** agondas glaucopis NHM Papua New Guinea: Oro Province, Kumusi River **I** agondas agondas (previously *E. a. bioculatus*) NSYSU Indonesia: West Papua, Sorong **J** agondas melagondas MCZ Indonesia: West Papua, Sorong **K** agondas melagondas MCZ Indonesia: Papua, Aru **M** agondas thryallis NHM Papua New Guinea: New Britain **N** agondas thryallis MCZ Indonesia: West Papua, Yapen **O** cybele cybele NHM Indonesia: North Maluku, Bacan.

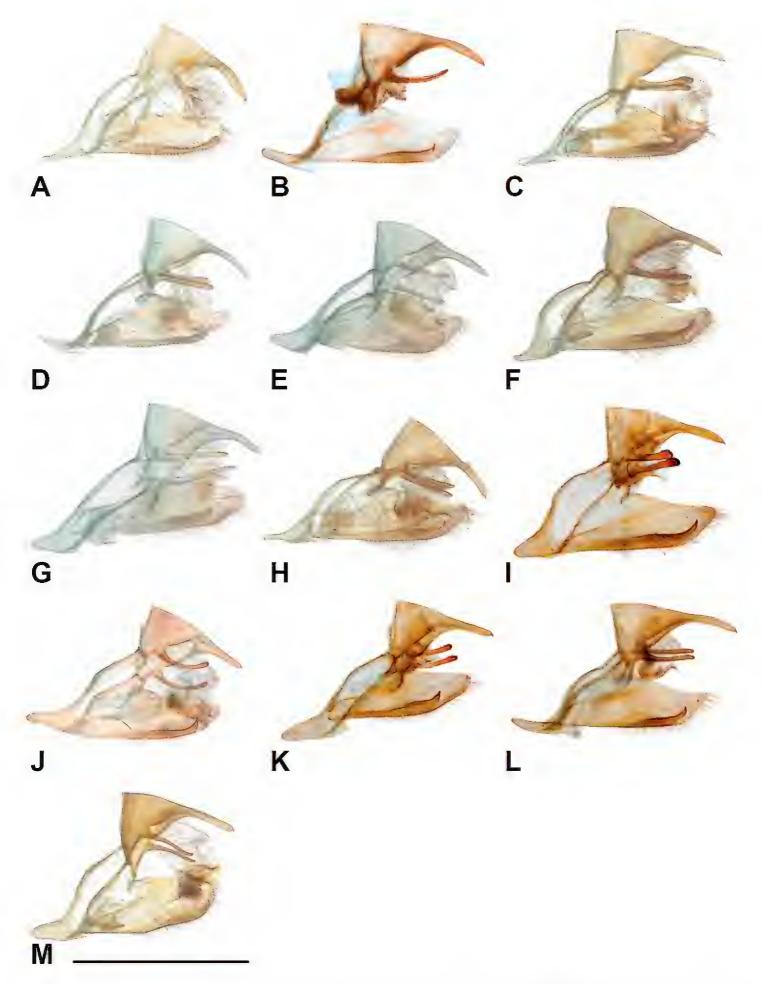


Figure 26. A cybele cybele NHM Indonesia: North Maluku, Halmahera **B** cumaea toliana MCZ Indonesia: North Sulawesi **C** hewitsoni meliophila NHM Indonesia: Maluku, Kisar **D** mimalon mimalon NHM Indonesia: Sulawesi **E** hicetas hicetas NHM Indonesia: Sulawesi **F** hicetas hicetina NHM Indonesia: Sulawesi **G** holofernes NHM Papua New Guinea: New Britain **H** bornemanni NHM Indonesia: Central Sulawesi, Banggai **I** phrikonis MCZ Indonesia: North Maluku, Sula Regency, Sanana **J** sangira NMNH Indonesia: North Sulawesi, Sangir island **K** umbratilis MCZ Indonesia: Papua, Biak **L** resplendens MCZ Indonesia: Central Sulawesi, Palu **M** singhala NHM Sri Lanka

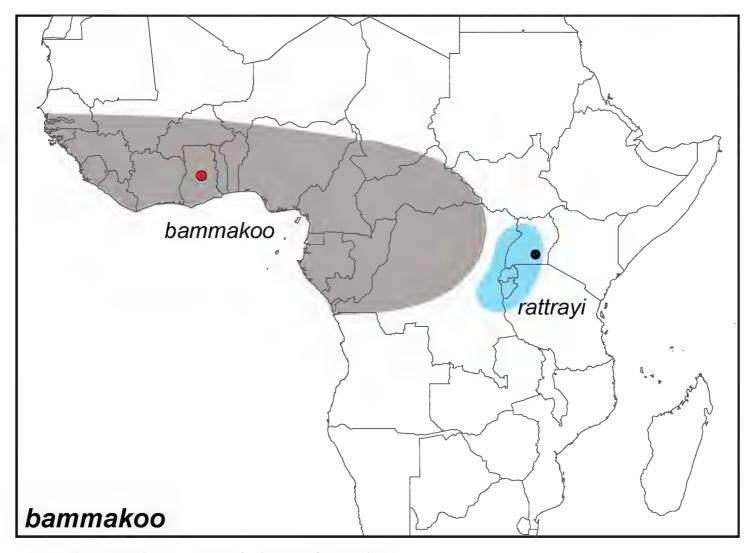


Figure 27. Distribution map of *Elymnias bammakoo*.

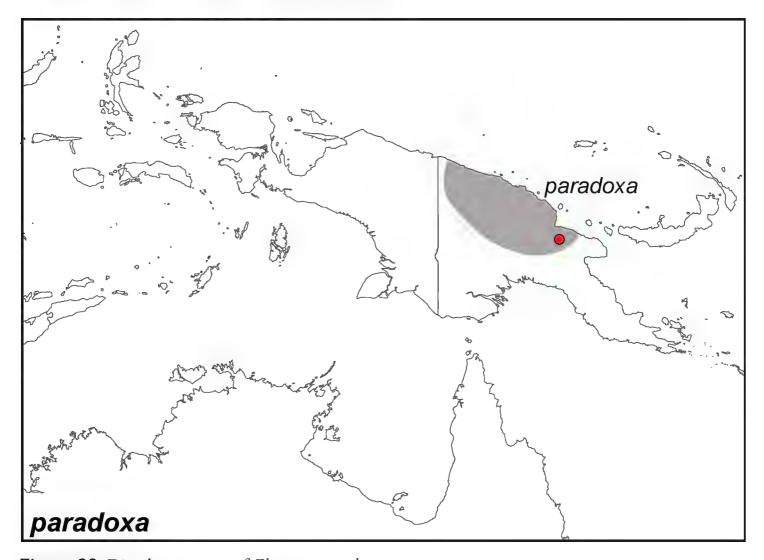


Figure 28. Distribution map of *Elymnias paradoxa*.

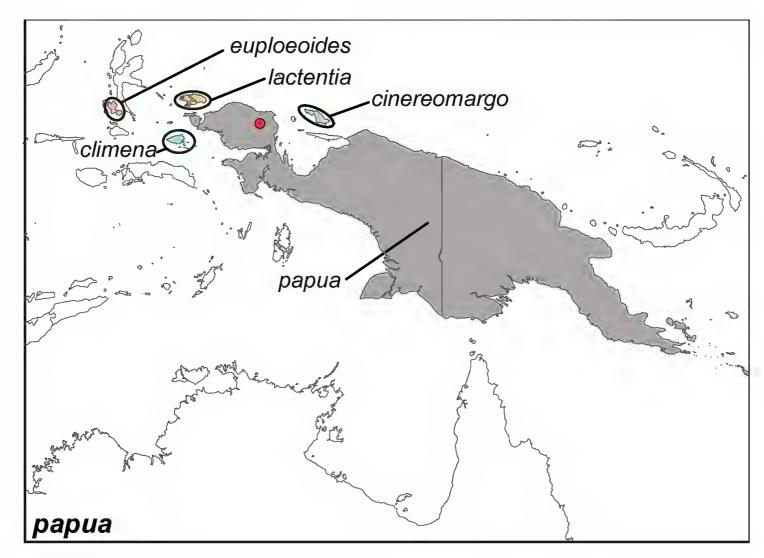


Figure 29. Distribution map of *Elymnias papua*.

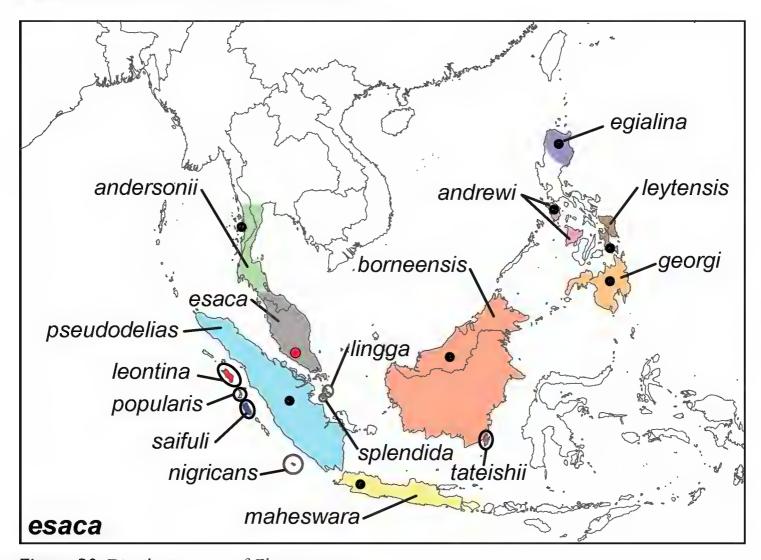


Figure 30. Distribution map of Elymnias esaca.



Figure 31. Distribution map of Elymnias vasudeva.

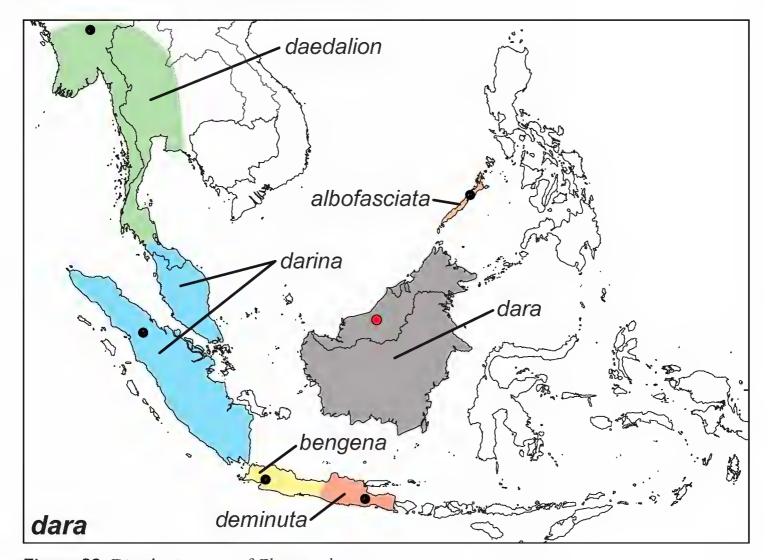


Figure 32. Distribution map of *Elymnias dara*.

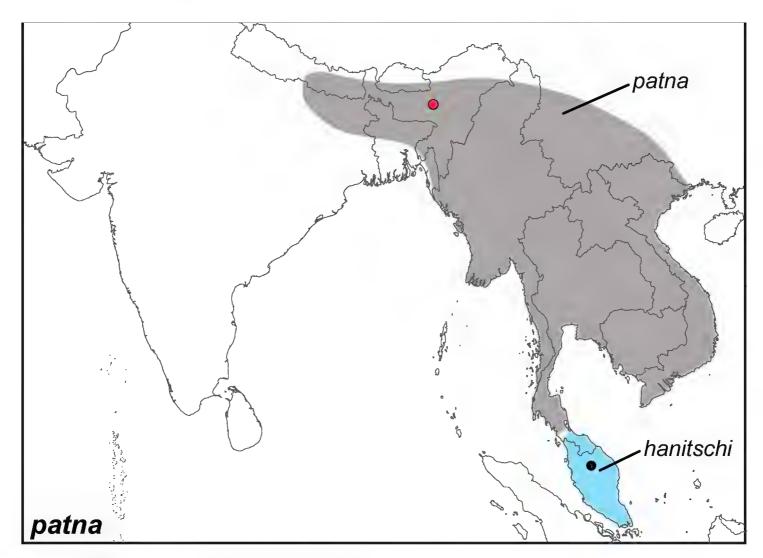


Figure 33. Distribution map of *Elymnias patna*.

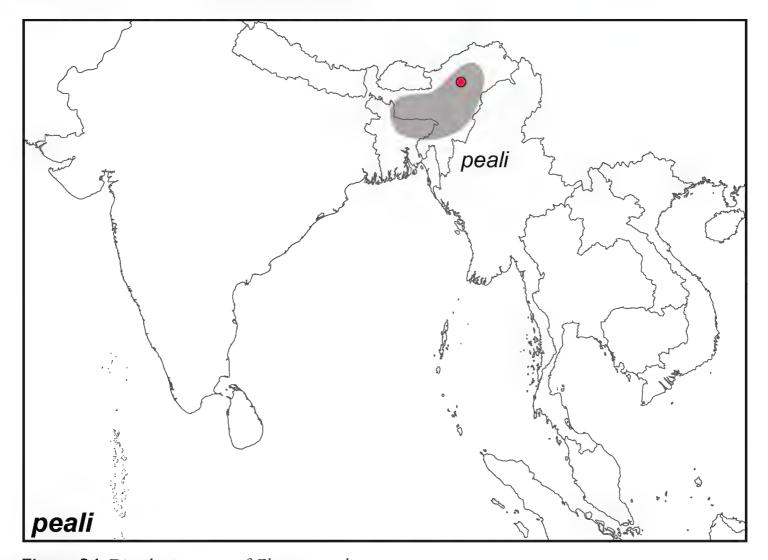


Figure 34. Distribution map of *Elymnias peali*.

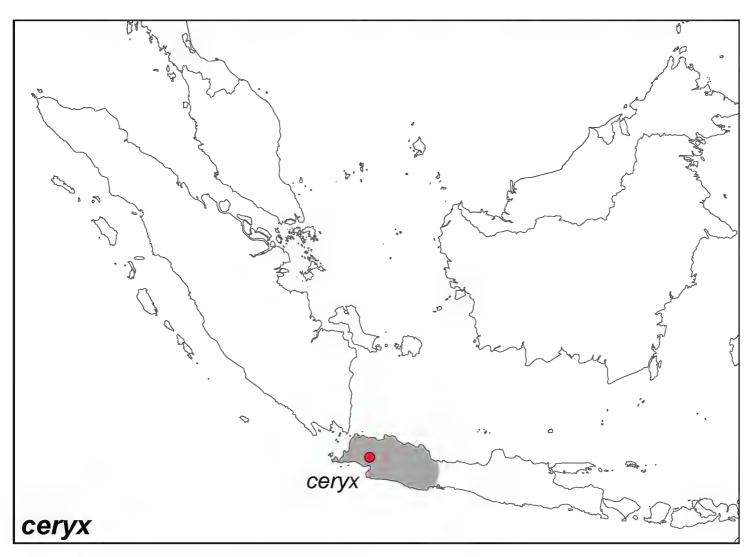


Figure 35. Distribution map of *Elymnias ceryx*.

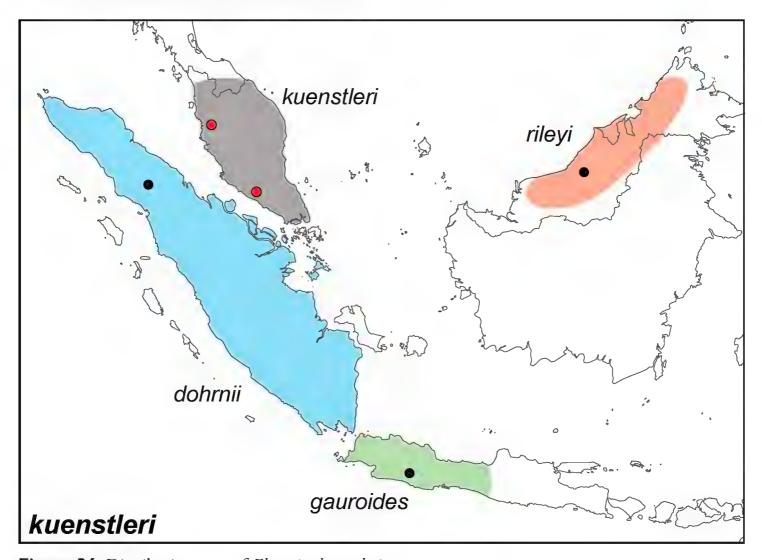


Figure 36. Distribution map of Elymnias kuenstleri.

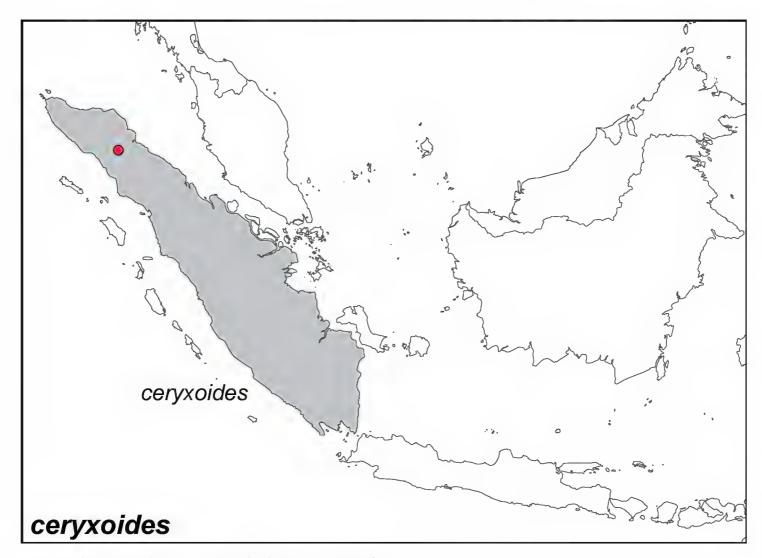


Figure 37. Distribution map of *Elymnias ceryxoides*.

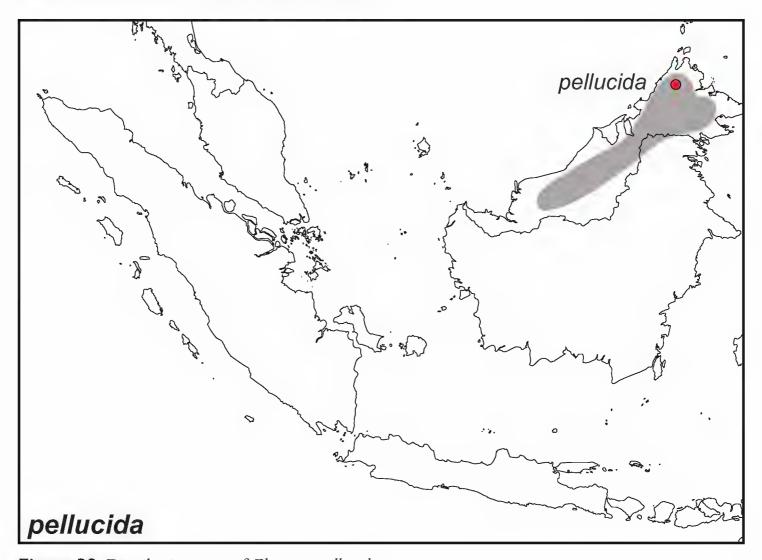


Figure 38. Distribution map of Elymnias pellucida.

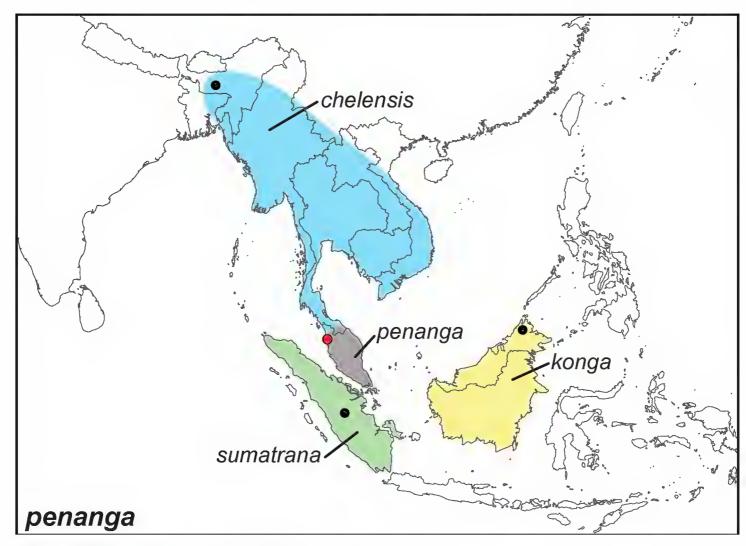


Figure 39. Distribution map of Elymnias penanga.

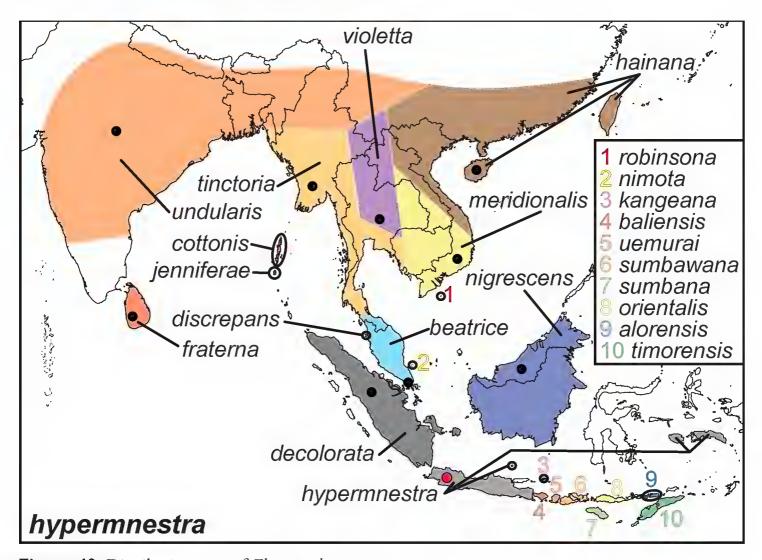


Figure 40. Distribution map of *Elymnias hypermnestra*.

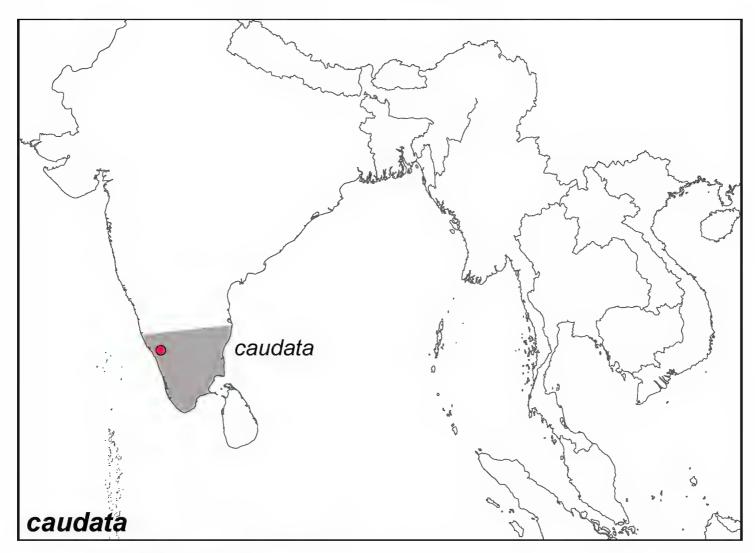


Figure 41. Distribution map of *Elymnias caudata*.

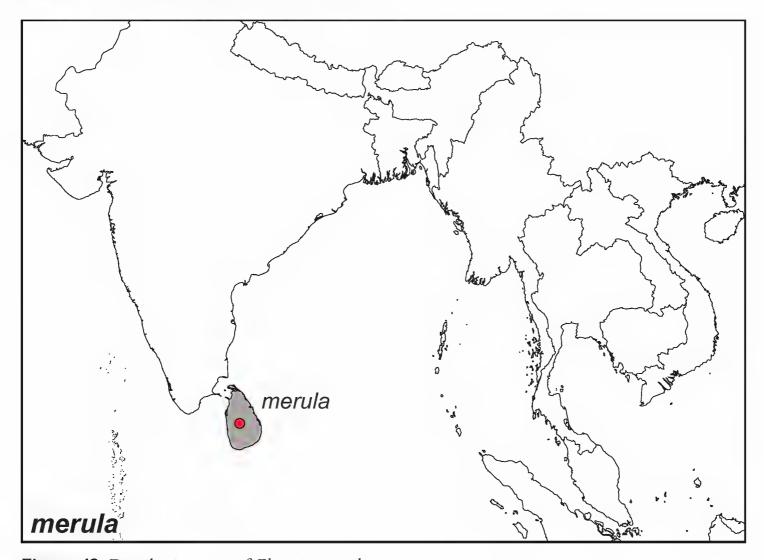


Figure 42. Distribution map of *Elymnias merula*.

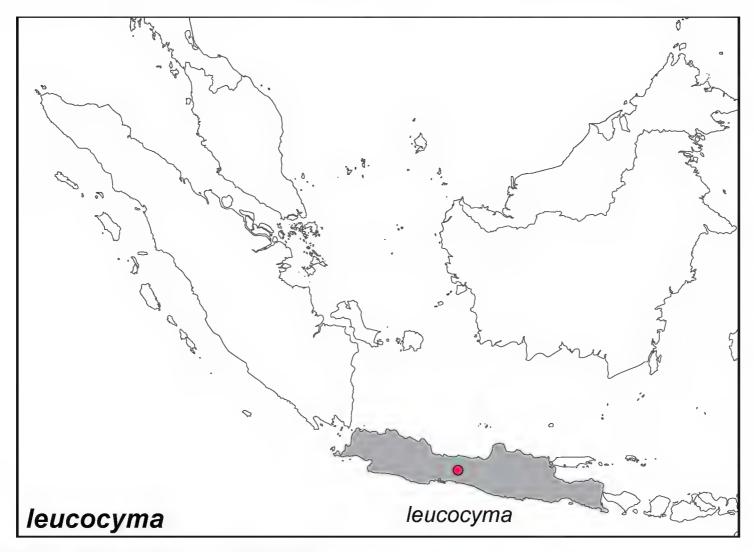


Figure 43. Distribution map of *Elymnias leucocyma*.

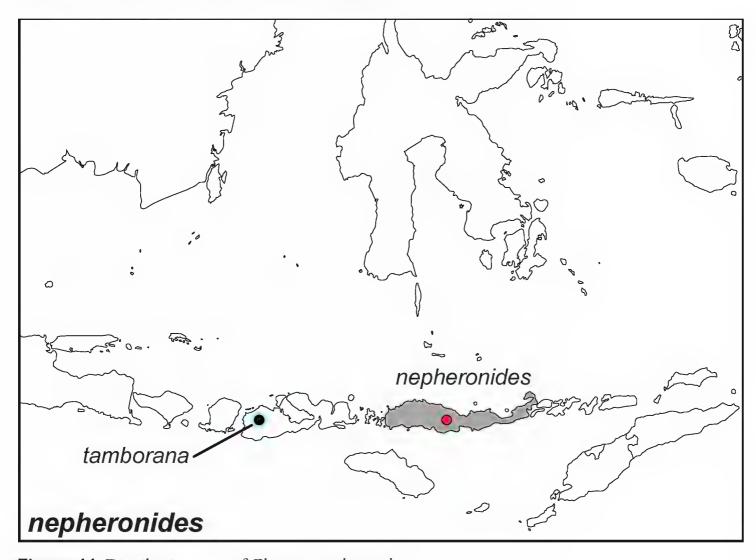


Figure 44. Distribution map of *Elymnias nepheronides*.

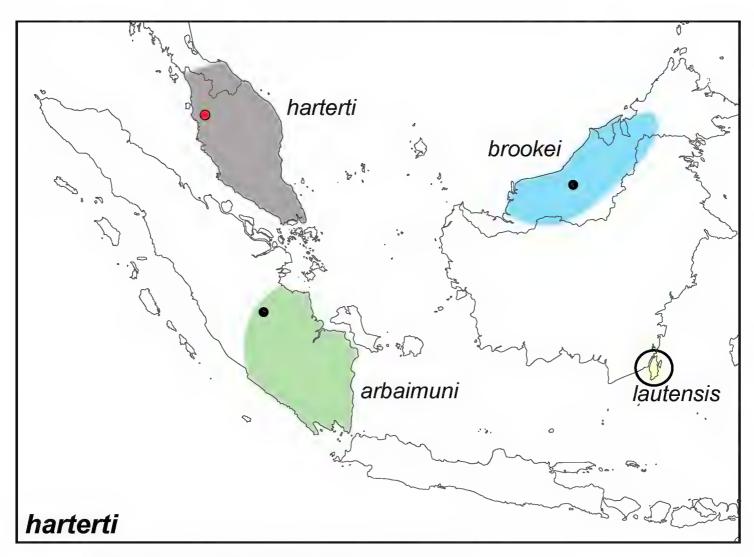


Figure 45. Distribution map of *Elymnias harterti*.

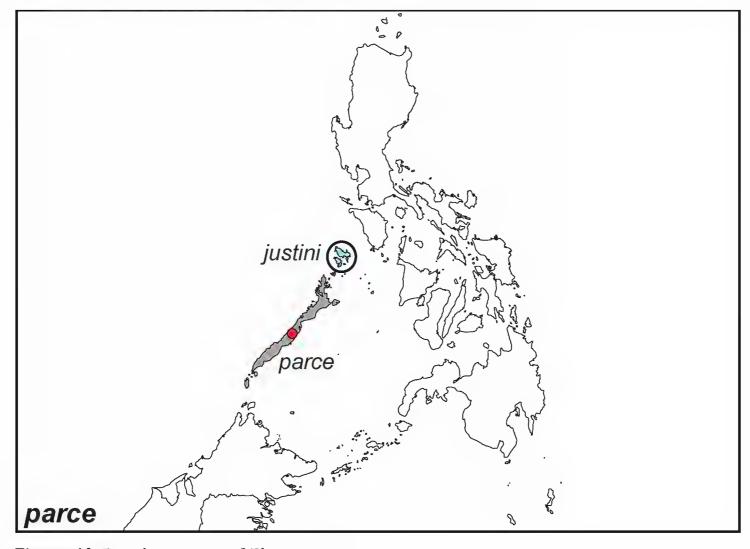


Figure 46. Distribution map of *Elymnias parce*.

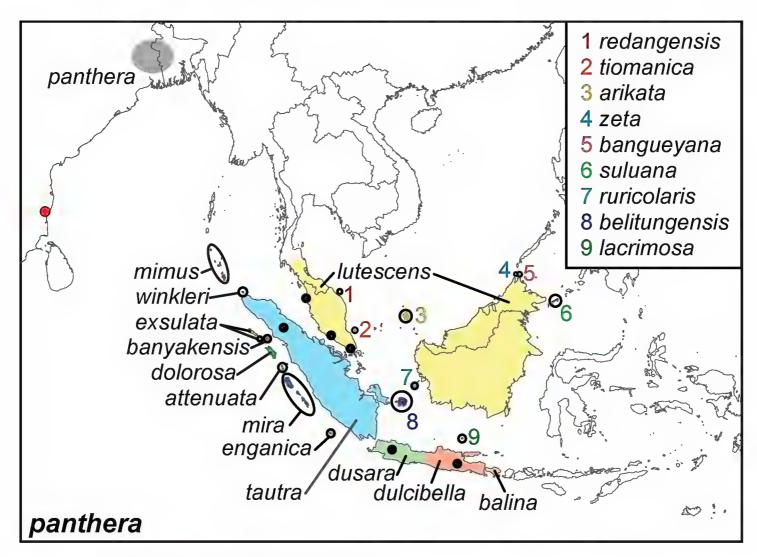


Figure 47. Distribution map of *Elymnias panthera*.

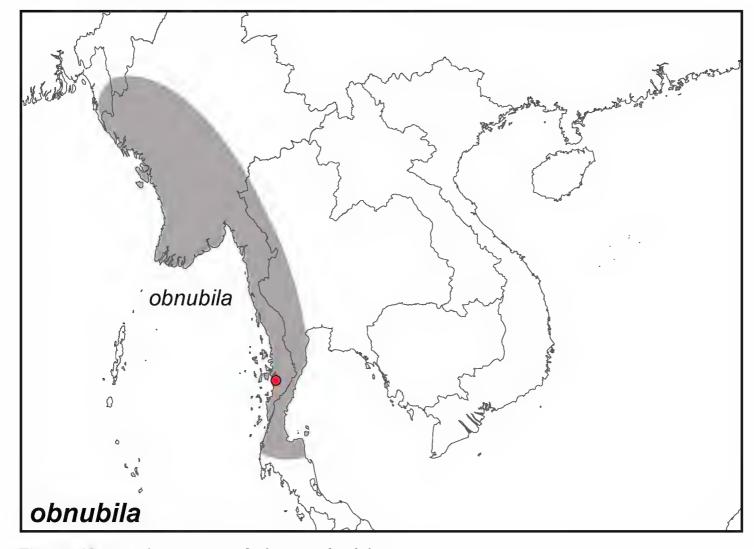


Figure 48. Distribution map of *Elymnias obnubila*.

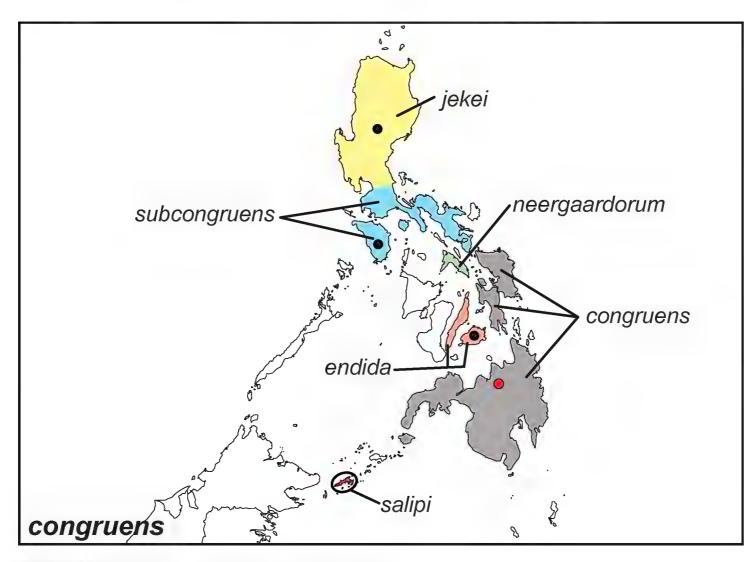


Figure 49. Distribution map of *Elymnias congruens*.

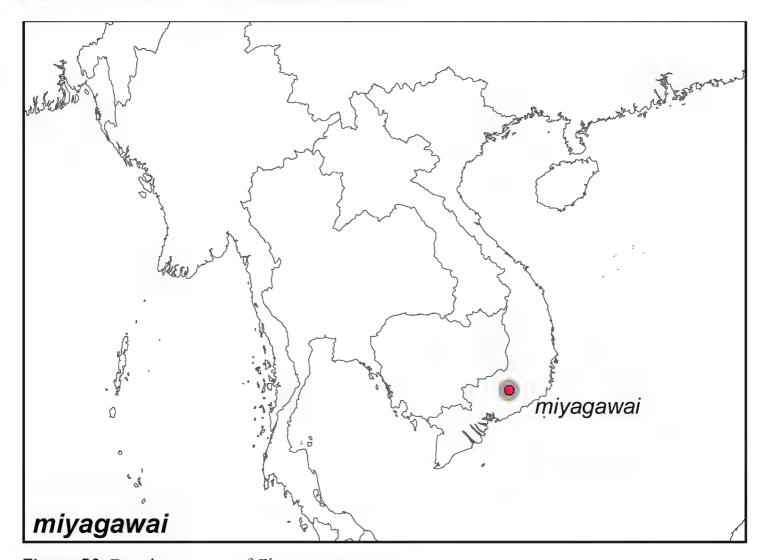


Figure 50. Distribution map of *Elymnias miyagawai*.

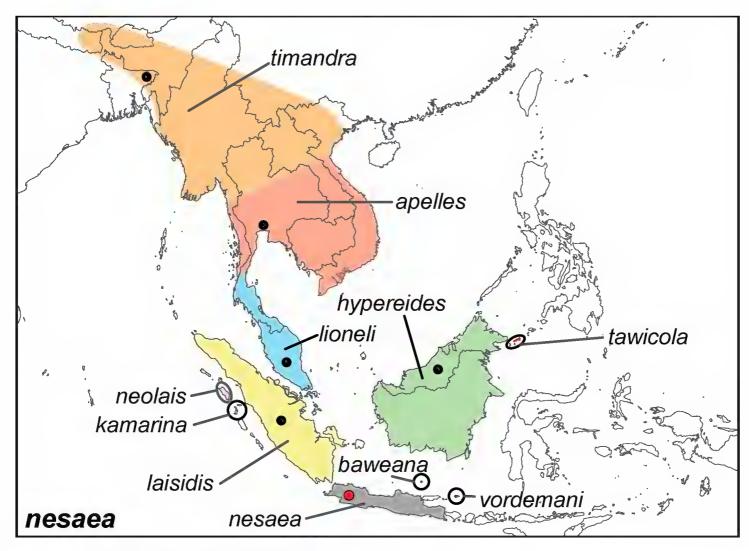


Figure 51. Distribution map of *Elymnias nesaea*.

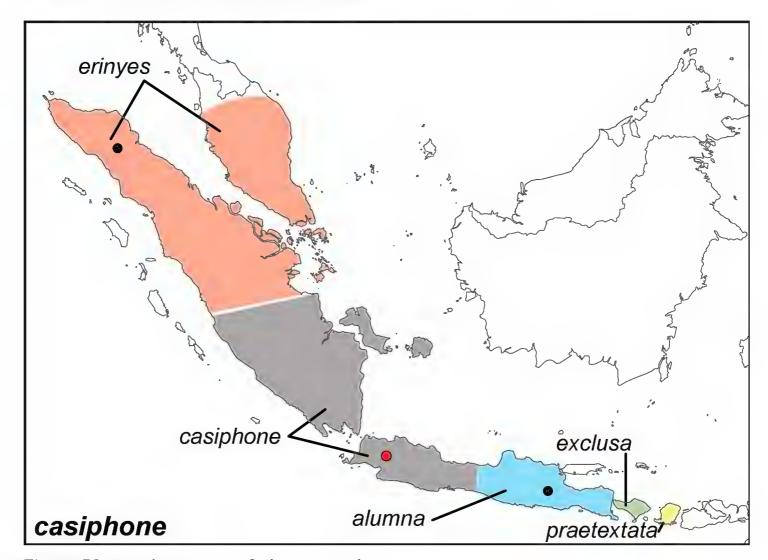


Figure 52. Distribution map of *Elymnias casiphone*.

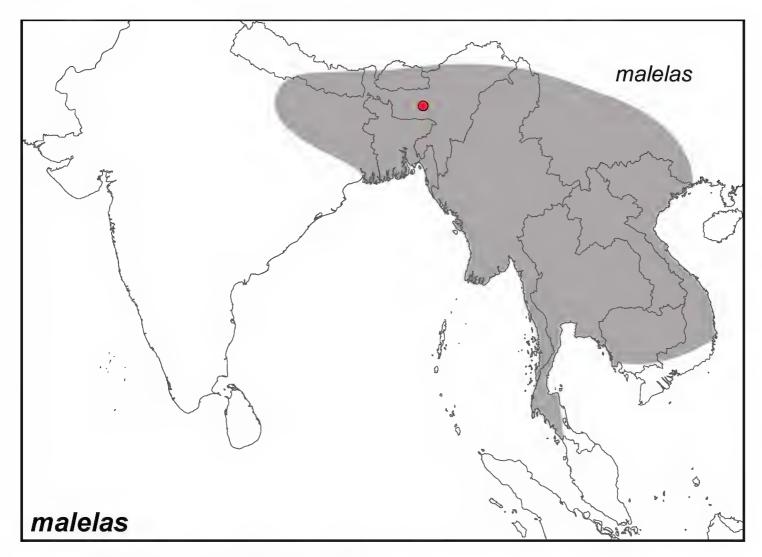


Figure 53. Distribution map of *Elymnias malelas*.

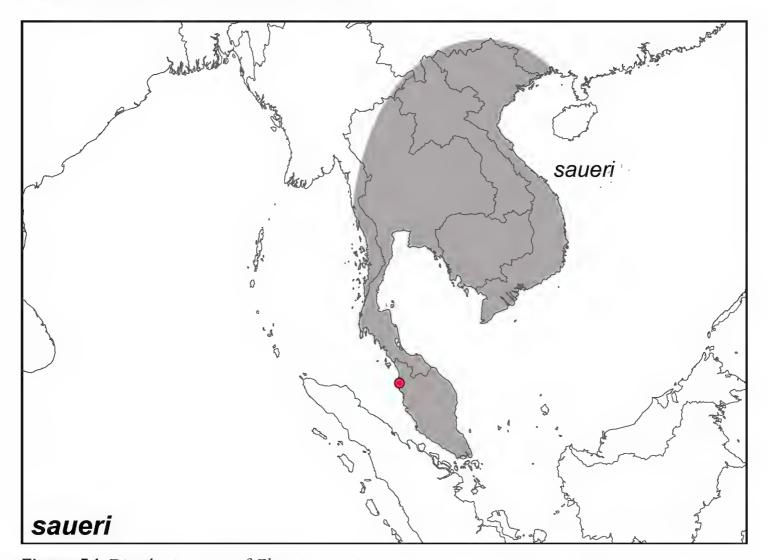


Figure 54. Distribution map of *Elymnias saueri*.

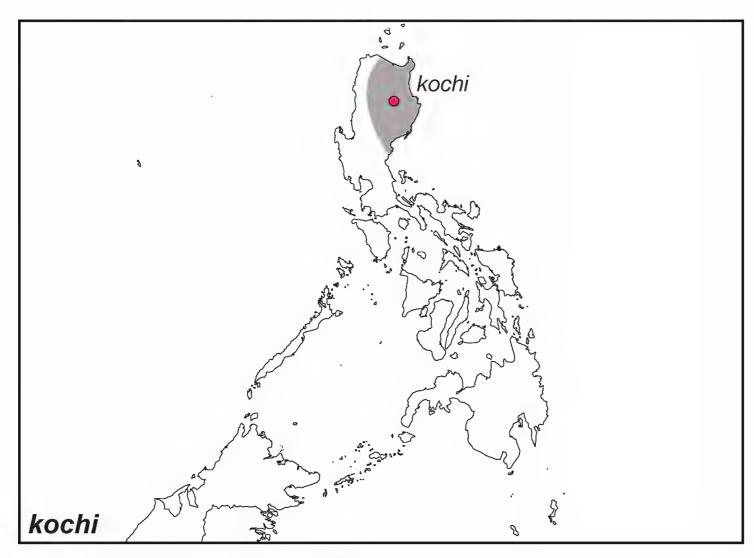


Figure 55. Distribution map of *Elymnias kochi*.

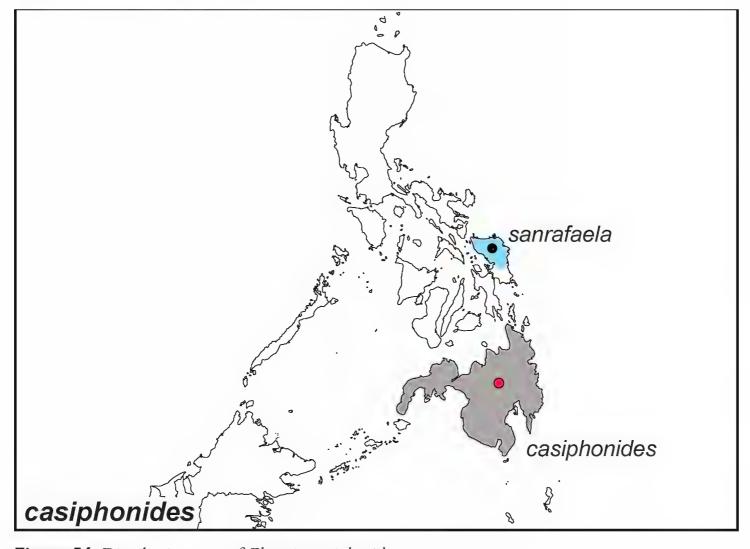


Figure 56. Distribution map of *Elymnias casiphonides*.

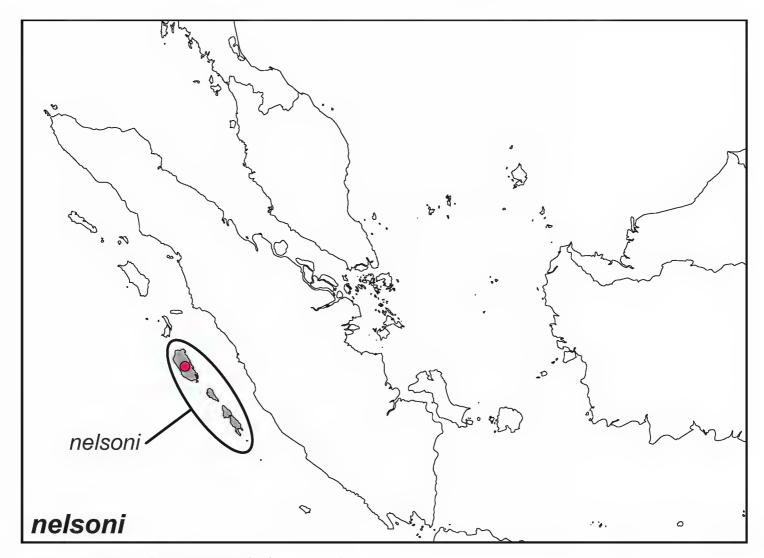


Figure 57. Distribution map of *Elymnias nelsoni*.

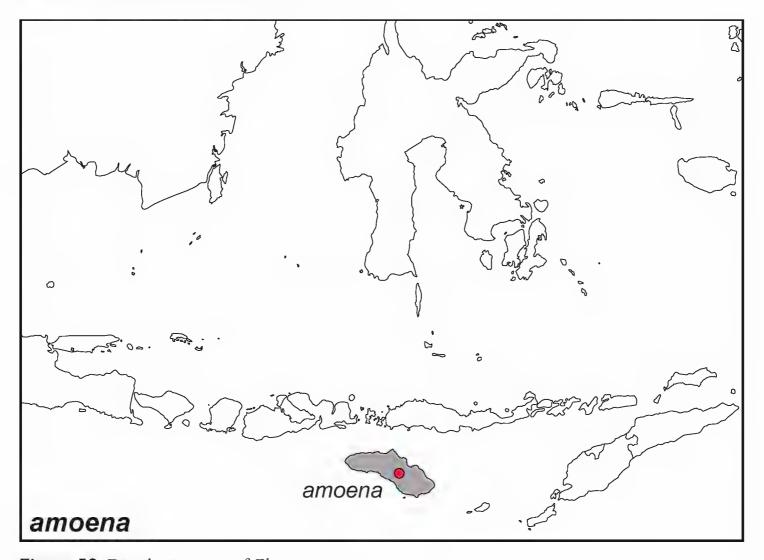


Figure 58. Distribution map of *Elymnias amoena*.

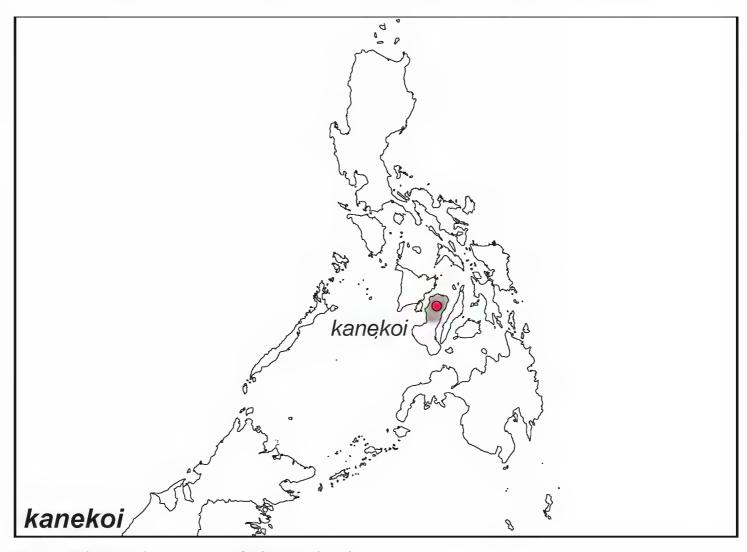


Figure 59. Distribution map of *Elymnias kanekoi*.

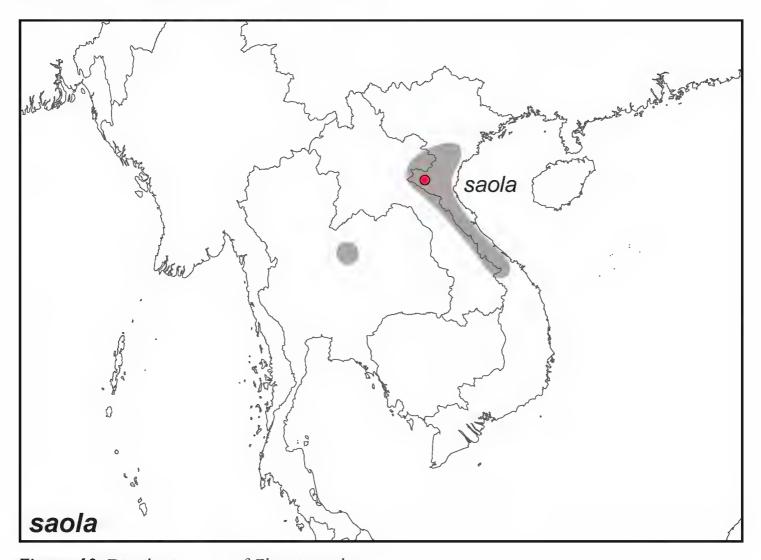


Figure 60. Distribution map of *Elymnias saola*.

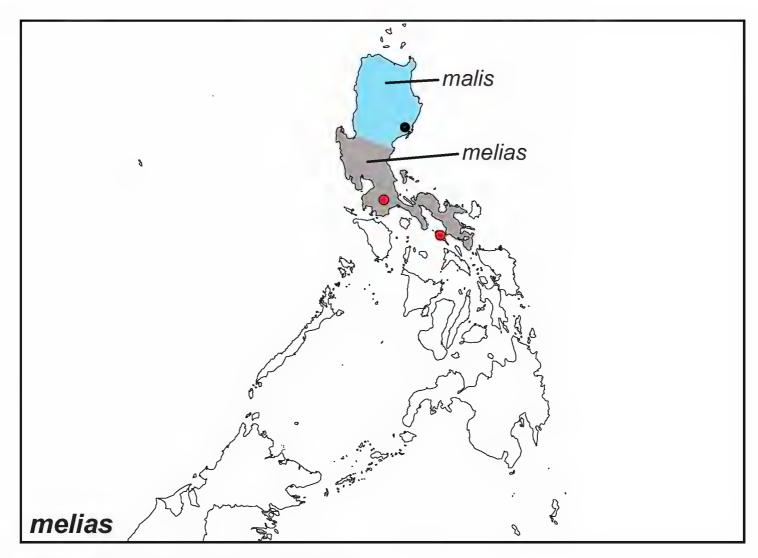


Figure 61. Distribution map of Elymnias melias.

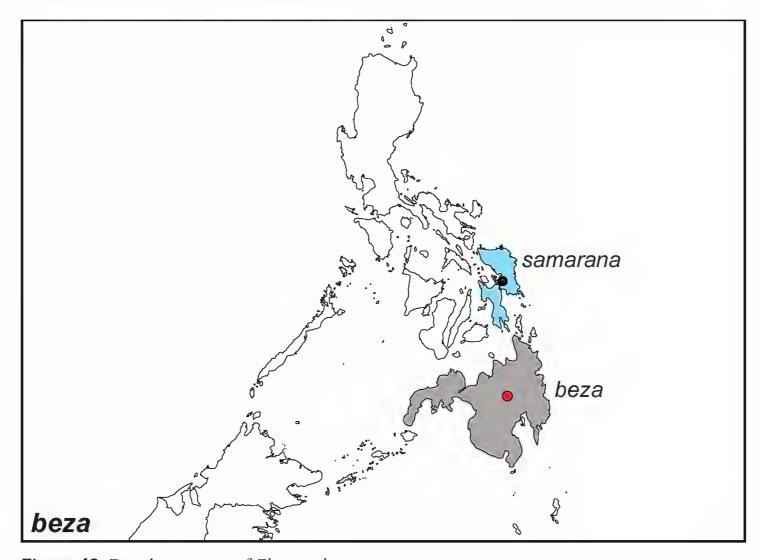


Figure 62. Distribution map of *Elymnias beza*.

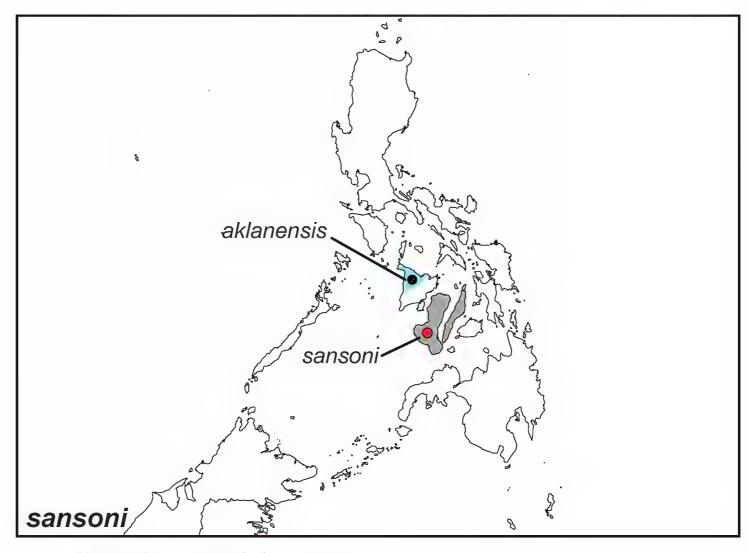


Figure 63. Distribution map of *Elymnias sansoni*.

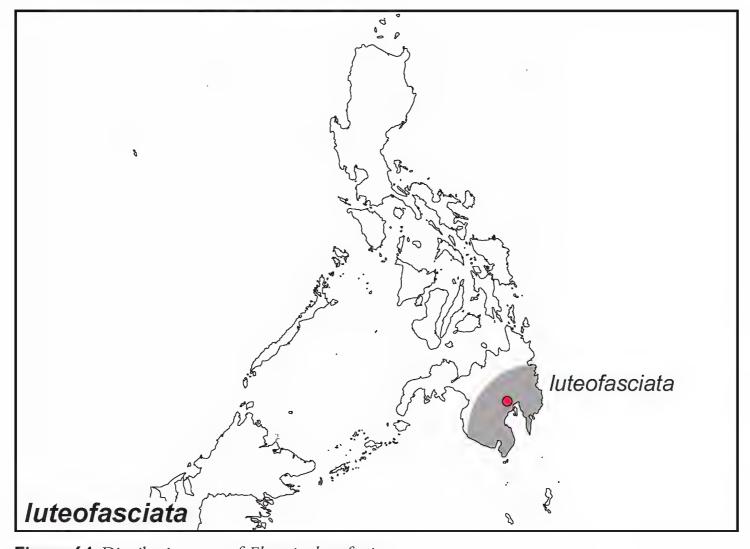


Figure 64. Distribution map of *Elymnias luteofasciata*.

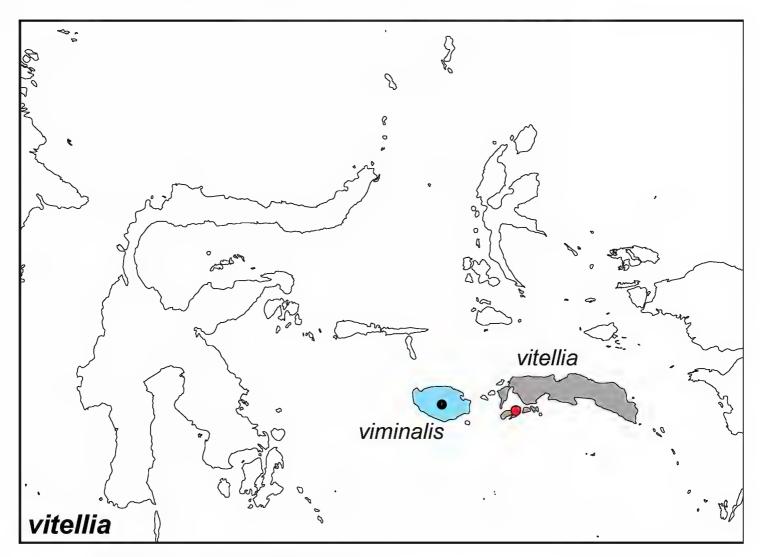


Figure 65. Distribution map of *Elymnias vitellia*.

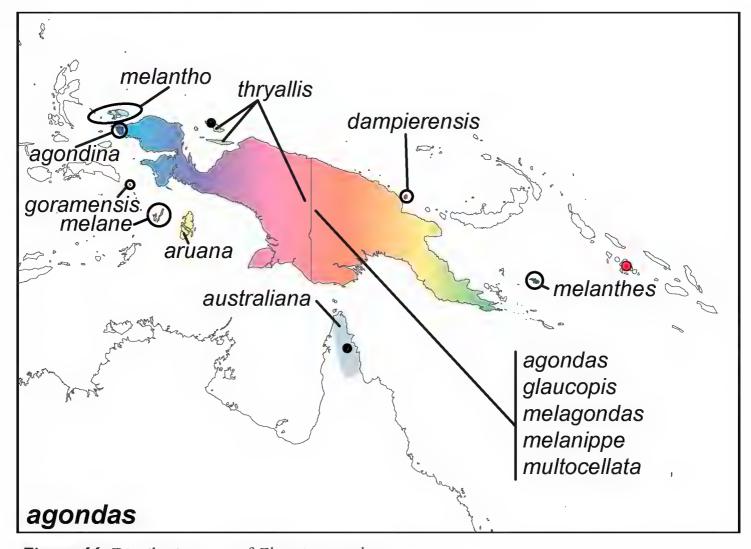


Figure 66. Distribution map of *Elymnias agondas*.

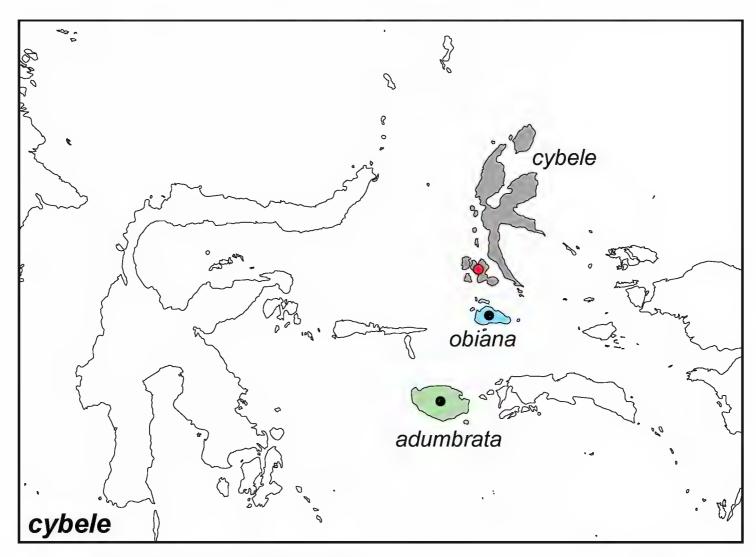


Figure 67. Distribution map of *Elymnias cybele*.

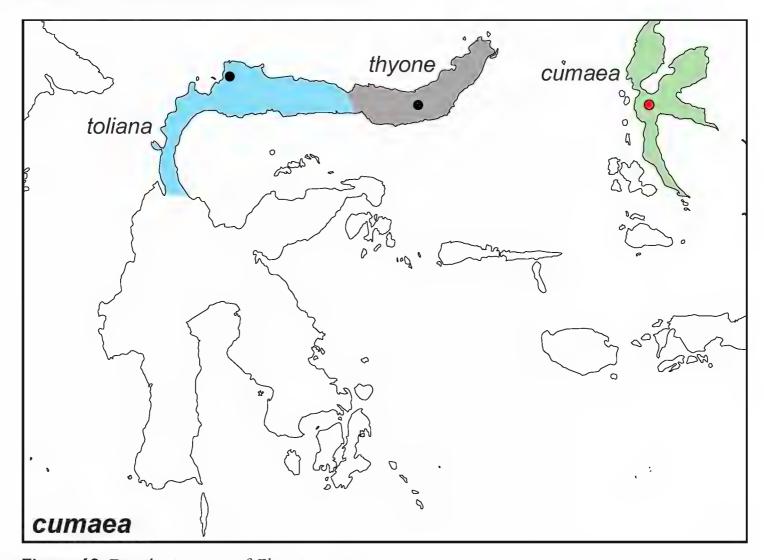


Figure 68. Distribution map of Elymnias cumaea.

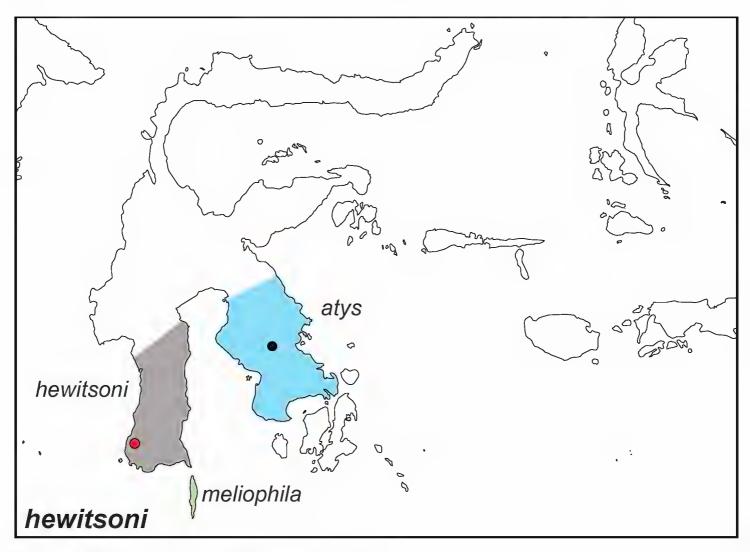


Figure 69. Distribution map of Elymnias hewitsoni.

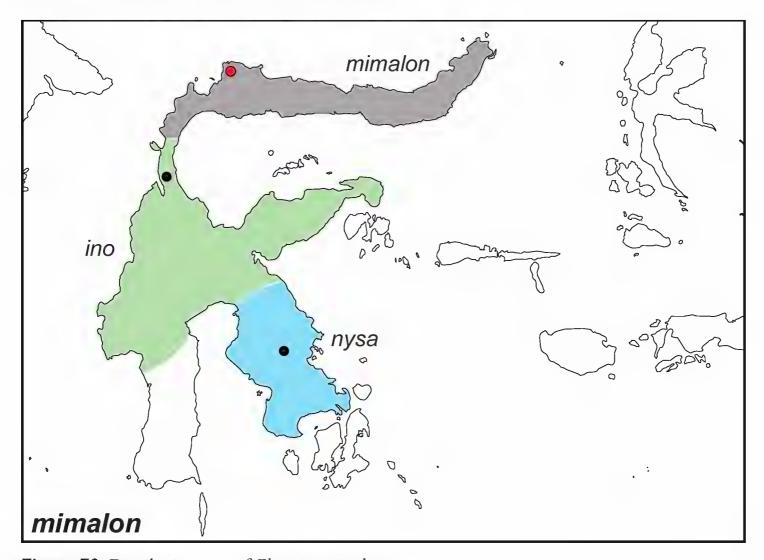


Figure 70. Distribution map of *Elymnias mimalon*.

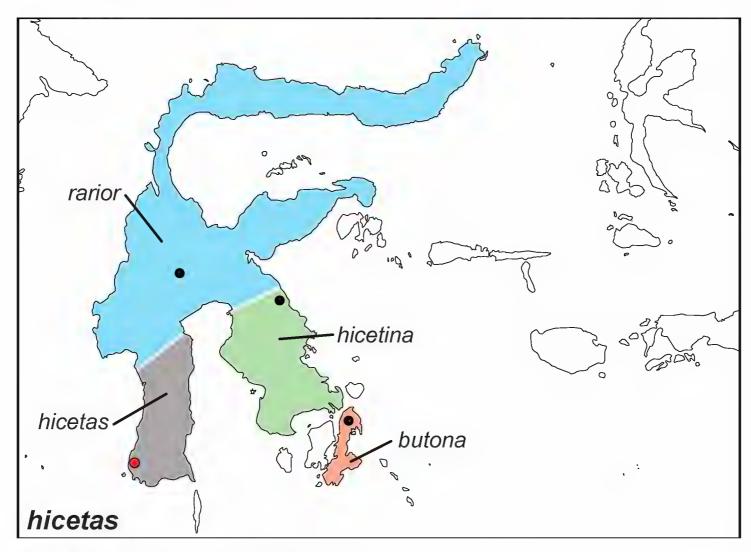


Figure 71. Distribution map of Elymnias hicetas.

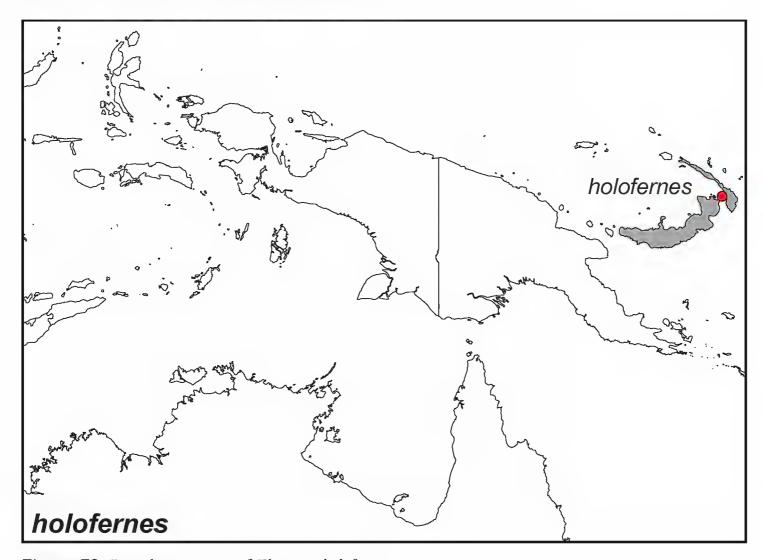


Figure 72. Distribution map of *Elymnias holofernes*.

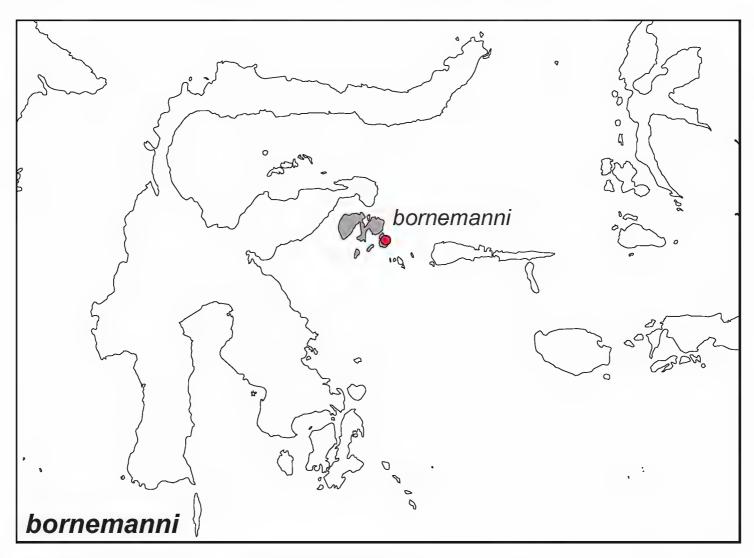


Figure 73. Distribution map of *Elymnias bornemanni*.

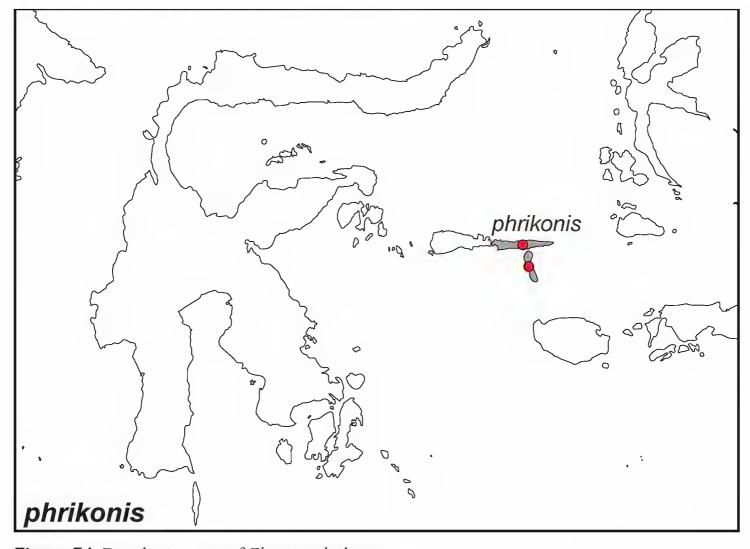


Figure 74. Distribution map of Elymnias phrikonis.

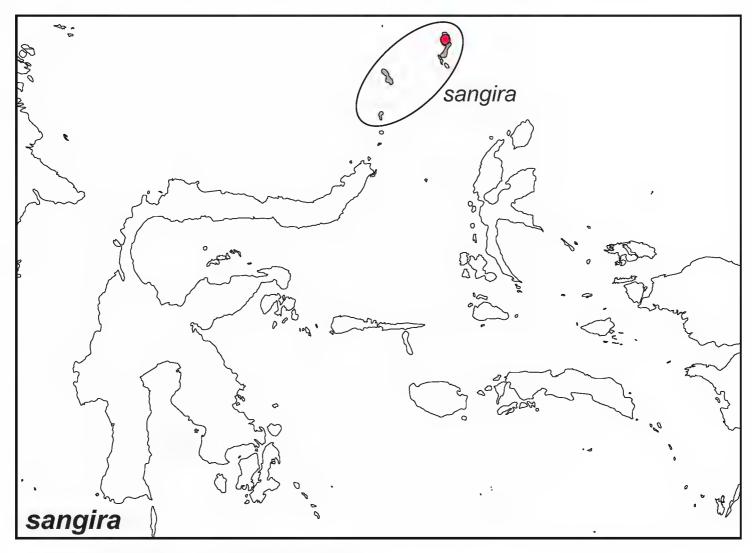


Figure 75. Distribution map of Elymnias sangira.

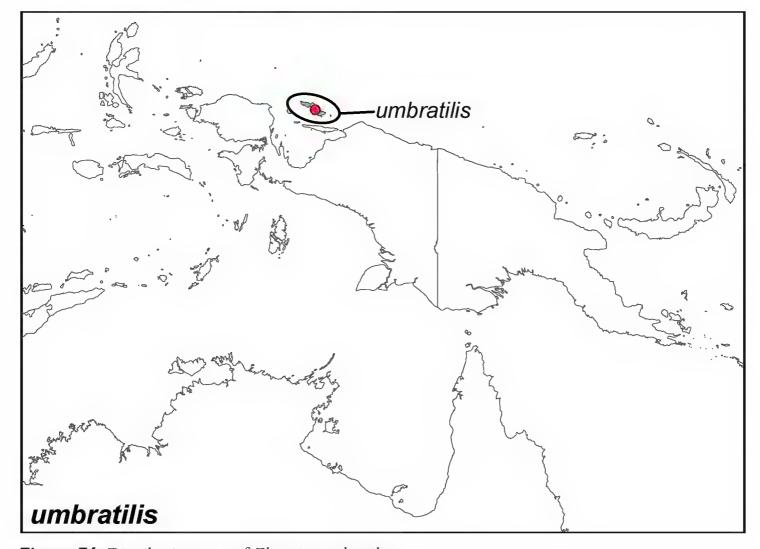


Figure 76. Distribution map of *Elymnias umbratilis*.

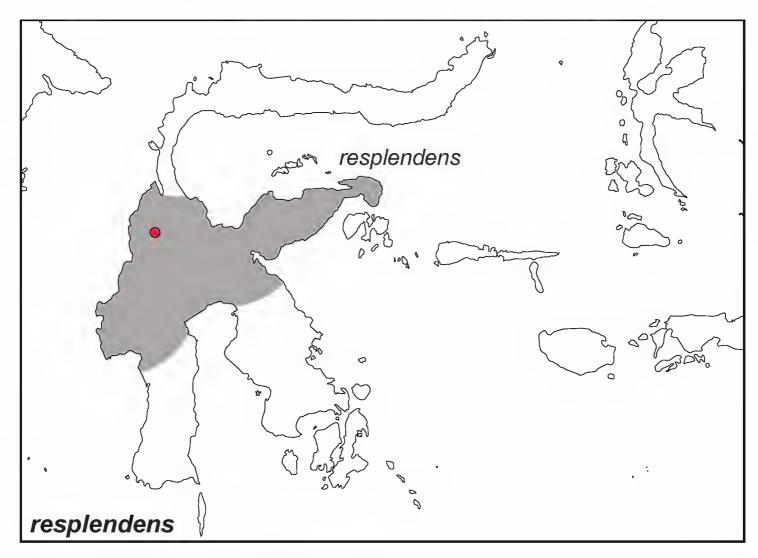


Figure 77. Distribution map of Elymnias resplendens.

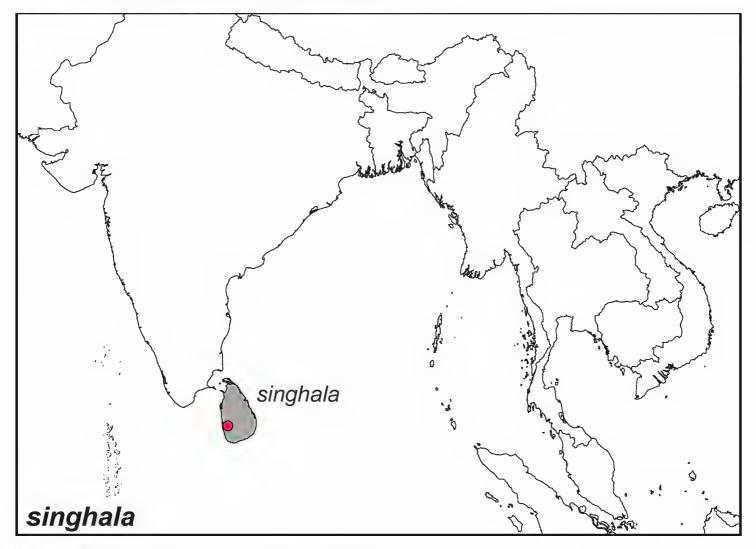


Figure 78. Distribution map of Elymnias singhala.

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